Contributions to Systematic Bryology

Dedicated to Lewis E. Anderson

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LEWIS ANDERSON, A TRIBUTE FROM A FRIEND AND COLLEAGUE[1]

HOWARD CRUM[2]

Legend has it that Alexander Evans resented obituary-like tributes to the extent that he dropped bryology in favor of a new and distinguished career in lichenology. I scarcely think that Lewis Anderson, retiring in the spring of 1982, will abandon the mosses that have engaged his interest for 50 years and, judging from outrageous and irascible comments adjusted to the heat of argument or the humor of the moment, I doubt if he would take up lichens.

I have known Andy for 30 years. Jack Sharp, Bill Steere, and Margaret Fulford have known him much longer. Andy is a complex person, and each of us has had a different view of him. I can only tell about the person I have known—kind and helpful, witty and charming, clever and resourceful, well informed and articulate, devastating in debate. It is difficult to write about a friend or to evaluate his career when he is still capable of making rebuttal. We have had a spritely correspondence which I might make use of, but much of our humor, gossipy and uninhibited, ought not to be lifted out of playful context.

The title page of our *Mosses of Eastern North America* is graced by illustrations of *Bryoandersonia illecebrum* and *Bryocrumia andersonii*, both endemic to the area under consideration. The association of generic names is pleasantly symbolic of our friendship and collaboration. *Bryoandersonia* was described by Harold Robinson in honor of his professor, but it was I who suggested that Harold work on the family to which the genus belongs. Andy named *Bryocrumia* in order to put an end to our long-standing disagreement as to the relationship of the genus. In a similar way I described *Brachymenium andersonii* to end a tiresome quibble about its generic affinities.

Our friendship has been based on mutual interests, scientific and cultural, as well as mutual tolerance for personal foibles, his and mine. We have a similar way of viewing the world and each other, with puckish good humor. We have a similar taxonomic skepticism. Our collaboration has been made lively with banter and derision. It has been a Mutt-and-Jeff relationship. I was the big dumb one, but not always!

Andy once accompanied my bryophyte class to Tahquamenon Falls in Michigan's Upper Peninsula. He regaled the class by funny stories about my erratic driving. (That was the year my lichen class gave me a St. Christopher medal.) Already at some disadvantage,

[1]I am pleased to acknowledge assistance from Pat Anderson for family photographs and personal insights. Professor Gerald Linderman of the University of Michigan helped with the interpretation of symbols representative of military successes. Photographs were supplied by Marjorie Watkins, Pat James, Jerry Snider, Allan Fife, Joseph Rohrer, and H. A. Miller.

[2]Herbarium, University of Michigan, Ann Arbor, Michigan 48104.

I further lost composure when an Indian woman got entirely too familiar while I was trying to lecture my class about bark epiphytes. That and many other stories have been told and retold at my expense, to friends, colleagues, students, even my children. Andy tells a good story!

He can get away with outrageous things. When we left Fort Churchill after a summer of living and working at the post, we were required to circulate a clearance form to supply, billeting, transportation, and the like. In answer to the standard query: Reason for requesting separation? Andy declared, "I am sick of this —— —— place." Of course, that was true and all they needed to know, but it was a chancy type of humor to try out on the military. When we left we stole a huge transparent bag full of cheese, crackers, cookies, and fruit. We looked like refugee immigrants with our "Central European Bag," but the goodies helped us tolerate a long train trip from Churchill to Winnipeg and Port Arthur and a car trip from there to New England. We took it with us when we went for a beer, everywhere. We were still lunching from it in our motel in Canaan, Vermont, when we were supposed to be taking part in a foray of the American Bryological Society in Canaan, New Hampshire. Actually we enjoyed being lost. We had an excellent supper and spent the next day on Mt. Monadnock and then joined the foray. Andy said, "This is just the sort of story Jack Sharp will enjoy. He will tell it everywhere." He did.

Once, in Florida, we pulled off the highway to study the map and have a beer. Too late we noticed that the police had set up a road block just downhill from us and, in fact, a police car was headed up the hill toward us. Having some notion that drinking beer in an automobile might be a no-no, we quickly hid the beer. We had an amiable chat with the officer who decided we had no criminal involvement or intent. I felt relieved at the simple outcome of the investigation and then startled when Andy presented the officer with a postcard boldly proclaiming. "Your visit has climaxed an already dull day!" As I said, Andy can get away with these things; the officer was amused and did not become surly or abusive, as one tends to expect! (Police brutality?)

Andy first met my wife when she and I were no more than friends, and I had had no reason to mention our friendship to him. He took her hand and said, "Oh, Howard said you were clammy." Of course, I had not, and she wasn't. He told me later that McCarthy (as we called her) would make a good wife, but she was too smart to marry anyone like me. I took pleasure, months later, to append to a dull business letter "Oh, yes! I am getting married next week." He had to telephone to find out that it was McCarthy. (He sent an embarrassing gift.) Years later I said I could just hear him telling Bill Steere, "Irene has been good for Howard. She has humanized him. And God knows he needed humanizing." With a guilty look that I have never seen before or since, he said, "You've been talking to Jerry Snider." I hadn't. I merely made it up so that I could trap him.

Andy loves an argument, no matter what the subject or the point of view. I rarely risk being out-competed, but I occasionally take pleasure in put-downs. Andy is an admirer of Thomas Wolfe's autobiographical novels, all with the theme, Ah, lost! and by the world forsaken! Part of his interest is centered on the locale. Old Catawba is North Carolina, and Andy once stayed at the Asheville rooming house run by Wolfe's mother ("Eliza Gant"). I have more than once taken delight in saying that Wolfe is the sort of thing I have outgrown. A similar violence was once evoked by saying that *Lolita* is amusing and not supposed to be taken seriously, didn't you know? Whether in argument or confrontation of other sorts, Andy is hard to beat out. Once he was driving at night on a notoriously

The early days in Mississippi, with Ike Shankle (the very best friend) and May Herndon.

dangerous stretch of road between Ottawa and Montreal. A driver coming toward us failed to lower his lights. Saying "I'll fix him!" Andy pulled over on the other lane. We were barreling toward destruction when, Thank God, the lights dimmed and the lane was cleared.

Andy is 10 years older than I and 10 times smarter, yet we have had from the beginning a comfortable sense of equality. I was once surprised to hear one of his students say that he was intimidated by the irascibility that I consider zestful. I first met him when I was a graduate student at the University of Michigan. Perhaps in 1948 he gave us a talk about teaching botany with an ecological bent. His talk was particularly well received in comparison with one on the Ohio State Method (an incursion into university teaching along the lines of progressive education). Andy is an effective lecturer, and he created the impression that he was indeed a skillful teacher at the introductory level. Certainly he was

Andy's mother. Andy at Mississippi State College, in ROTC uniform.

experienced. He once told me that he had taught general botany so long that he could back into a class, without preparation and in the nude, lecturing on any subject. After the lecture a number of Bill Steere's students were invited for an evening of good stories, some of them poking fun at Bill. I have often been at a similar disadvantage when Andy has told my students that they need to be de-Crummed.

I met Andy again, briefly, at the Columbus meeting of AIBS, in 1950. I have never, until this day, told him that I missed the bryologists' foray because I stupidly got on a bus full of pteridologists. Andy was there with H.L. Blomquist. Bloomy was a kindly person, famous at that time as the victim of one of Fernald's friendly critiques. He was just back from the botanical congress in Stockholm and had much to tell, in much detail, about the trip. Both he and Andy made me feel that even a graduate student (feeling oafish about missing the foray) was worth bothering with.

It was in the spring of 1953, when I was at Stanford working with Bill Steere, that Andy came out with Virginia Bryan to help Bill on a study of moss chromosomes. Bill had had some experience with the cytology of *Petunia* and some involvement, obliquely perhaps, with Bob Lowry's study of the cytotaxonomy of *Mnium*. Virginia had worked with Lowry on *Trillium*, and since her husband had recently taken a position at Duke University she had spent some time with Andy but not on the cytology of bryophytes, as far as I remember. Andy had done his doctoral research on the mitochondria of higher plants. They made an effective team. They learned together the techniques of handling meiotic

figures. The problems were great; the chromosomes were minute, they clumped, they stained too much or too little, and especially small chromosomes had to be distinguished from mere fragments on the basis of "behavior." Not the least of the problems was finding sporophytes in the right stage of development. They worked hard. Bill kept up with the writing as fast as counts were made. The published results gave important stimulus to this type of research, partly because of the information on methodology. Bill used this work as a standard for comparing chromosome numbers in temperate and arctic floras (and found no significant increase in polyploidy in the arctic), and he spent some time with Andy in 1956 counting chromosomes in mosses of northern Manitoba. Virginia did a number of important cytotaxonomic works on her own and some with Andy. But it was Andy who went on to become the acknowledged leader in the cytotaxonomy of mosses. Yet it was he who told Bill on his arrival in California: "If you get me interested in this stuff, I will never forgive you." Andy has always worked with meiotic figures. When the Japanese cytologist Inoue visited Durham many years later, he taught Jerry Snider his techniques for doing mitotic counts but told him that Andy was too old to learn!

I was often included in some of the less structured activities of the chromosome counters, field tripping to the coastal redwoods and the sierras, sampling California wines, eating Lobster Newburg on the wharf at Monterey while watching sea lions catching fish thrown out to them, and enjoying a concert in San Francisco (when the tympanist was missing for the Drum Roll).

Just before showing up in California, Andy collected mosses in the Ozarks. In the summer of 1954 I went to Duke University to help name the material gathered on that and other field excursions. I was glad to be paid, even though it came out of a petty cash fund. It was very hot, and I had only woollen clothing. I was going to Ottawa in September and naïvely thought I wouldn't need summery clothing again. Competing with Rudy Schuster's typist for the use of a fan, we spent long hours together with microscopes set up side by side. We exchanged ideas and information while checking our concepts against specimens in Grout's herbarium. It was out of this experience that we became acutely aware of the need for an improved version of Grout's *Moss Flora of North America*. From that first step the *Mosses of Eastern North America* evolved. We worked on a major paper on the phytosociology and phytogeography of Ozark mosses, still not finished! We did produce, however, a study of the Funariaceae and a miscellany of taxonomic contributions.

We made a trip to the coast with Henry Oosting. We tried to sleep on the floor of a laboratory at the Beaufort Marine Biological Station, but stifling heat forced us to spend the night on a pier. (We interrupted a tryst already in progress.) I did very much enjoy learning something about the ecology of the coastal plain from Oosting and observing the close friendship between him and Anderson. We later went to Florida, to the Gainesville meetings, with Heinie Oosting, Bill Culberson, and Terry Johnson. Heinie used up his patience with me, owing to middle of the night disturbances resulting from sophomoric humor, enjoyed by everyone but Heinie. Of course, the situation would not have arisen except for Heinie's cautious use of the dollar, which resulted in our sleeping five to a room. (The details of the disturbance were related to my incredulous children 30 years later.) Heinie was also violent about the unexpected expense of replacing his smooth old tires and a lack of sympathy he detected among us. Heinie's rages were not to be taken very seriously. They, in fact, added fun. On field trips one adjusts to inconveniences. The

Graduation from the University of Pennsylvania in 1936. The 1940 photograph appeared in the Duke University year book labeled Louise Anderson.

humor often meets the needs of the moment and rarely bears repeating. It can be crude, sophomoric, or both. Heinie's violent outbursts were accompanied by humor, and Andy's light touch certainly helped us weather the storm. Heinie told me that it was always fun to go to meetings with Andy, because he knew everyone and brought something of interest out of everyone.

It was good for me to spend a summer at Durham, as I had just become editor of *The Bryologist*. Andy was serving, unofficially, as the business manager and had recently arranged to have the printing done there by the same firm that did *Ecological Monographs*, of which Oosting was an editor. He also had recently arranged for reprinting the back issues of *The Bryologist* and (with help even more anonymously from his wife) took care of the sales that eventually resulted in a degree of financial solvency that the journal still enjoys. Andy had, of course, been meaningfully involved in the American Bryological Society for years. He was curator of the Society's moss herbarium and therefore a member of the executive committee—from 1936–81! He served as President in 1950–51. Because he arranged for Duke University to purchase the Grout Herbarium, he continued to serve the taxonomic needs of the Society in an important, though indirect way, as well. But most important of all, he has fostered the family feeling that characterizes the Society.

During that summer I stayed at a dormitory inhabited by noisy and boisterous divinity students, but I often visited the Andersons and their five children. The family had been

Currituck Point, North Carolina, with A. J. Grout (holding a bouquet) and Alexander W. Evans, in 1939. Dr. Evans was especially concerned with Cladinas of the Coastal Plain at the time. *Cladina evansii* is a special feature of the North Carolina coast. Dr. Grout twitted Dr. Evans about the fact that the moss flora, with all its faults, was (or soon would be) done, whereas Evans's scholarly studies on liverworts were never pulled together into a really useful form. It has been said that Evans was discouraged from putting out a liverwort flora of North America because Frye and Clark's compilation introduced too many problems for easy solution at the end of Evans's research career.

planned, two children before the war and two after, but the last one turned out to be twins. Andy had a large vegetable garden and took good care of the lawn on Sunday mornings when Pat and the children went to Sunday School at the Methodist Church. The house was small and cramped. It was later much expanded with a "necking room" overlooking the backyard for teenage daughters, but soon afterward, about the time the children left home, they moved to a beautiful, spacious "geriatric" home where Pat's passion for birds and flowers was finally unfettered. In the new home is a marvelous Steinway grand piano. In the old house were two grand pianos, smaller than the Steinway, sitting side by side. Pat didn't have time to play, and the children didn't show a great deal of interest in learning. With fewer responsibilities Pat eventually recaptured and developed her skills, playing classical music and rag. Music was a special feature of the environment. Andy had a good

In the Navy. Aboard the *U.S.S. Hancock*; bombs figured on the wall represent air missions (as opposed to much more numerous sorties); the large group of Nippon flags represent war planes downed; the flags at the upper left represent naval vessels destroyed, those to the right merchant vessels. On shore, Andy driving a Jeep.

collection of classical recordings, heavy on Italian opera, and good high-fidelity equipment. At a later time, when he spent a winter with me in Ottawa, we were both taken up by the relative merits of Maria Callas and Renata Tibaldi. We liked Renata better, but for dramatic clout on or off stage, who could touch Callas?

Pat and Andy were obviously devoted to their children and to each other. The children were quiet and pleasant but not obviously regimented. Pat's talent for order and efficiency, though unobtrusive, made for a calm and restful environment. I particularly enjoyed the homemade ice cream that was often a feature on hot Sunday afternoons.

Through the 1950's I continued to visit Durham during the winters. Andy and I continued our studies in the Grout Herbarium. Rudy Schuster was still there in the mid-fifties. We sometimes went to the Little Acorn for a greasy, beery meal, sometimes to give Pat a rest from the need to feed us. One time Rudy, Bill Culberson, and Terry Johnson joined us. Rudy, like many voluble and volatile persons, had a few beers (really very few) and passed out with a silly grin on his face. Like many voluble and volatile wives, Olga put him under the shower when we got him home. A few days later Rudy went to Ann Arbor to interview for a job, and we sent him a telegram saying that we missed him at Christian Endeavor (at the Little Acorn). I ruefully admit we were all adults!

In the summer of 1955 Wilf Schofield and I collected in the Canadian Rockies and mailed cytological material to Andy. Surprisingly the material survived the transport and the heat, and Andy got a large number of counts which we together published. The paper included some information on keeping material alive until counts could be made and also

on ways to hold back the meiotic events until counts could be made. These studies were continued in 1956 when Andy and Bill Steere joined Wilf and me at Churchill, Manitoba. We shared a room, for a time, with a sawfly specialist from the British Museum (which he, of course, called the BM). He thought Andy was a northerner and called on me, because of my midwestern drawl, to expound on sociological conditions in the South. Actually Andy is from the Deep South, from Mississippi cotton country, not I. He has little or no regional accent and none of the stock attitudes that are attributed to Southerners. For example, he thinks Southern cooking is vastly overrated. The reason for his cosmopolitan attitudes, racial and otherwise, may be that his family came to the United States, from England, during or shortly after the Civil War, and they saw the South from an outside point of view at a time when the southern social structure had collapsed. As a boy Andy was particularly influenced by his grandfather, who had little sympathy with the time-worn remnants of southern chivalry. Inappropriately or not, I once chose to tease Andy about his Southern background. We had spent a day on the tundra, near the coast where the horseflies were very troublesome, endlessly buzzing around one's head. I had long been near the breaking point. One of them even followed me back to camp where it abandoned me for a black soldier. The look Andy gave me was pure Mississippi—or at least that was the interpretation I chose. Incidentally the cytological results of that summer have yet to be published!

During my visits to Durham and especially during two collecting trips to Florida, we talked about revising Grout's *Flora*. Our intention was to make a quick and simple update. Grout's three volume work, begun in 1928 and completed in 1941, was a pioneering work of broad scope. It had some serious faults, obvious from the beginning, to Grout as well as to others. Grout had remarkable insights at the specific level but knew little and cared less about phylogeny. He surely never heard of Fleischer's views on sporophytic stability and gametophytic plasticity, and he seemed unaware of the generic and familial concepts so recently presented by Brotherus in Engler and Prantl. His concepts were not unlike those of Schimper's *Synopsis* well back in the preceding century. His descriptions he copied, adapted, or translated (in a clumsy way) from sources abroad. He was careless in determination of specimens, and so his range designations were inaccurate. He was provincial in his background and interests and had no feeling for the phytogeographic probabilities of distribution. Yet his flora with all its shortcomings helped lift bryology out of the amateur to a truly scientific level. Our objectives were to bring the nomenclature up to date (at a time when the *Index Muscorum* was not even begun), correct and otherwise improve the descriptions, add records of distribution, standardize the format, and perhaps supplement and replace some of the illustrations which Grout borrowed, mainly from the Europeans.

We soon realized that a useful revision of Grout's work would entail much more research than we had expected, and so we redirected our efforts toward a thoroughly original manual of a lesser geographic scope. We lived in the East and knew that flora best, and also the western and arctic floras presented some unique problems, inadequate collection among them. We therefore decided to concentrate on the eastern deciduous forest which extends from southern Canada to the Gulf of Mexico and from the Atlantic to the prairie grasslands. By a few additions from the periphery we could make the work more generally useful, while limiting ourselves essentially to an ancient flora of phytogeographic unity.

Lunch at Mont Tremblant, Québec, during the pre-congress foray of the bryological section. The other photograph shows Howard Crum with Lewis Anderson, Clare Davidson, E. Schelpe, and Lionel Jaffe.

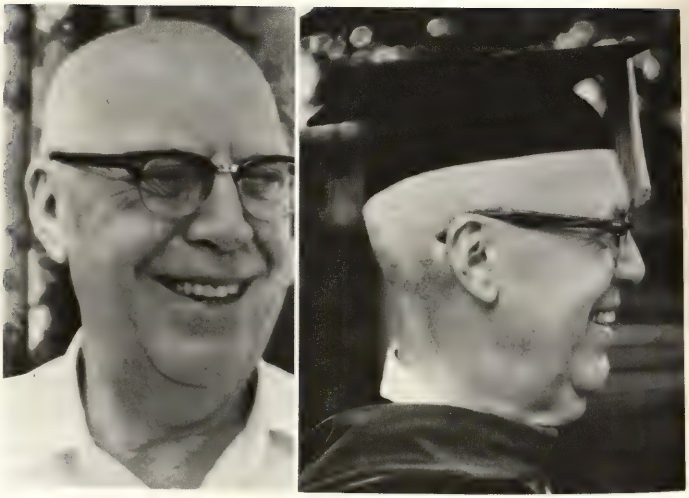
Work on our flora began in earnest in 1959 when Andy took a sabbatical leave and spent several months of a hard winter with me in Ottawa. He arrived by plane, with no wallet or any identification to get him through customs and immigration. He talked himself in. I was living there, as a bachelor, in a new house. Andy had imagined that I lived in some sort of boar's nest, but soon found out that there was no dirt in my house. We shared household chores, including a great deal of snow shoveling. I cooked, and Andy got fat. He later said, with some justice, that all my recipes started out with butter. He claims that we drank a good deal. This I do not remember, but some liquids *are* caloric! Andy was serving on a systematics panel for NSF at the time, and some of the work related to grant proposals was done in the evenings, perhaps with something liquid. Andy particularly enjoys telling that I said I did not know much about buying alcoholic beverages in Ontario, but when we went to a brewer's warehouse, all the working stiffs seemed to know me by my first name. The truth was that I had been in a hospital room with a cousin by marriage of *one* of the persons working in the warehouse.

Our procedure was to begin each species by studying specimens from outside our area, first those from abroad, then elsewhere on the continent. After coming to some understanding of the species as defined elsewhere and some feeling for allowable variation, we studied all available specimens from eastern North America, making from them careful observations from which detailed descriptions were compiled. We have been criticized, and perhaps justly so, for our "extreme conservatism." We certainly tried to get a global view of the species before deciding on its merits. So many of the standard treatments are based on the limited expressions found in small goegraphic areas. The truth is probably somewhere in between splitting and lumping, but I would make the further defense that we were writing a manual, not monographically revising every genus of the flora. We had no particular division of labor, except that in the interest of uniformity of style, form, and terminology, all descriptions were written by me, from notes provided by us both, although after 1959–60 we worked for the most part separately.

The manuscript went through at least three revisions. The illustrations were for the most part supervised by Anderson, who composed them into plates and numbered them at the very end of the project, about 25 years later! At the end we looked them over together, and Andy redrew or touched up as necessary. He also supervised the photocopying, done in Durham and sent on to the Columbia University Press. Altogether we had the use of five illustrators, two of them at the National Museum of Canada, three at Duke University.

And how about the cost? The National Science Foundation provided $252,000 in addition to a publication grant of $29,300. The research grants were made to Anderson and administered by Duke University as I was supported in research activities by the National Museum of Canada and later by the Herbarium of the University of Michigan. Although provided for a different purpose, my NSF grant for $59,252 made possible the afterthought inclusion of *Sphagnum*. It might be noted, as a token of appreciation, that Donald Richards offered to finance the publication, but Andy preferred not to take advantage of a friend if other means of finance could be found.

We were most fortunate in having the support of William C. Steere, who, as a member of the editorial committee for the Columbia University Press, was unquestionably instrumental in making publication possible. Even taking into account a friendly bias, some of Steere's remarks used by the Columbia University Press to document an



A recent view of a characteristic smile. In cap and gown at Marshall and Carol's graduation.

application for an NSF publication grant no doubt helped our cause: "There are no other American bryologists who could do the present work better. . . . We have here, then, the fortunate combination of the absolutely right authors and a topic that desperately needs treatment. . . . To sum up, this manuscript represents a splendid concept carried out by the most able and appropriate people in this country." Since I am sharing this praise with someone that I thoroughly respect, I feel reasonably comfortable about including this quotation. I hasten to add that we dedicated the work "To William Cambell Steere who guided, encouraged, and inspired" out of long-standing friendliness and respect, not because of these lavish comments.

Partly through support attached to the project, eight Ph. D. students were trained in bryology at Duke University, each contributing in some way to our understanding of the flora: W. B. Schofield (actually a student in plant ecology working under Oosting but very much involved in bryological activities), Virginia Bryan, Ardith Johnson, Harold Robinson, Marshall Crosby, Richard Zander, Jerry Snider, and Claudio Delgadillo. To this number, but after the writing was essentially done, can be added David Lane and Ann Stoneburner. My own students were less directly involved, but certainly Dale Vitt and William Buck made contributions of an important, though indirect nature.

In collaboration with Bill Steere we were able to publish a checklist of the mosses of North America, in 1966, revised in 1973. A third edition is pending. We had trouble with joint authorship, as it was rarely possible to discuss the many decisions about what to include and how. We felt some need to stay close to Grout's *Moss Flora*, as the only inclusive manual available to North American bryologists, even though that meant

A triptych view of a teacher in the coastal plain of North Carolina on a very cold day in February 1977.

continual compromise. We compromised ourselves in presenting concepts that none of us felt comfortable with. Andy and I were more conservative than Bill, and he eventually decided that the entire list should be entirely freed of Grout's ghostly presence and of his authorship. To our disappointment, he withdrew from our friendly collaboration.

An extensive cytological program carried out by Anderson paralleled our taxonomic studies. Studies on the chromosomes of various areas were made possible by NSF support. Much of this work is yet to be published in detail, owing to pressures associated with putting together the published flora, but the bare data are incorporated in that work. Incidental to such cytological studies, Andy compiled the most complete file anywhere giving information on chromosome numbers in mosses. Some of his work was done in collaboration with Matti Al-Aish, Virginia Bryan, Betty Lemmon, and Jerry Snider, as well as William C. Steere (and to an extent myself).

One spin-off result of our collaboration was my *Mosses of the Great Lakes Forest*. This manual, intended only for students at the University of Michigan Biological Station in northern Michigan, unexpectedly filled a greater need in North America and in Europe too. A third edition was published in 1983.

Our exsiccati set, entitled *Mosses of North America*, also grew out of our "manual labors." Five-hundred numbers were distributed on exchange to fifty institutions. An additional two hundred are ready for distribution (as of 1981).

We each brought to the project an extensive background of field work. Since the early 1930's Andy collected throughout the Southeast, especially in the Carolinas, including the Southern Appalachians as well as the Piedmont and the Coastal Plain. He visited Grout in Vermont, and he collected with Grout, Evans, and Blomquist in the Coastal Plain of North Carolina. Early in the 1950's he collected extensively in the Interior Highlands of Missouri, Arkansas, and Oklahoma. I had a more scattered experience, in Mexico, California, Alaska, the Yukon, the Canadian Rocky Mountains, and many parts of eastern North America north of the areas best known to Andy. Together we collected in Florida, Québec, northern Manitoba, northern Michigan, and New England. Andy made a trip to

The bryophytes class at Highlands Biological Station in 1979. The second photograph was made during the 1981 foray of the American Bryological and Lichenological Society, also at Highlands.

Africa and two to Europe. His experience in Europe is particularly noteworthy. The account of the 1978 annual meeting of the Nordic Bryological Society may be quoted (from *Lindbergia*, in 1980): "The promoters of the society, Elsa Nyholm (Sweden) and Lewis E. Anderson (USA), were assigned the first honorary memberships of the society. In the motivation the Council referred to the events which led to the initiation of the society and to the efforts to stimulate the society persistently shown by Elsa Nyholm on many

excursions and during her ten years' service in the Council. In 1964, when Lewis E. Anderson visited colleagues and herbaria in the Scandinavian countries, he suggested to Elsa Nyholm that activities of Nordic bryologists should be organized into a society, an idea which had not previously been thought of. Together, Elsa Nyholm and Lewis E. Anderson went to Copenhagen to discuss the suggestion with Kjeld Holmen. Letters to Antero Vaarama (Finland) and Per Størmer (Norway) made it possible to proceed, and two years later the founding meeting was held in Sweden."

A letter from one of the European trips gives some flavor of the man. Andy had tea with Verdoorn. He found that Florschütz had "the zaney quality that you and I like. He has a good sense of humor, can laugh at himself and at pompous colleagues." Bizot heard that he was in Paris and came up for a day. "Not a bad sort, actually—alas I thought of him as someone in his 90's or thereabouts, but actually he turns out to be about my age. Very blustery and better than I had imagined. Also Per Størmer has been here (Paris) for a couple of days. A kind of a Blomquist, but also younger than I had imagined—also about my age. Nice, modest, very quiet person. Madame Allorge is a curious and interesting and very nice person—actually one of the nicest persons that I have ever known. . . . The wrong bryologists have been here. We have had no one over here to defend American bryology. To the extent that I can defend our quality I am doing good—and as you know I can do it loudly and vigorously, and I hope without rancor."

I should explain that we argued about senior authorship. Neither of us cared, but Andy convinced me that Crum and Anderson sounded better, for some reason, and that had been the order of authorship in most, if not all, of our joint publications.

Andy has been very helpful to me in my *Sphagnum* studies. We made several trips to the North Carolina mountains and Coastal Plain. He knows those species very well, having been exposed to H. L. Blomquist both as teacher and colleague. We once made a particularly good trip to the Coastal Plain of North Carolina. We found all the species of interest and had brought back material for microscopic study. I had just returned home when Dick Andrus visited, and Andy took him on exactly the same tour and showed him exactly the same populations. It was reported to me later that Dick was greatly impressed with how well Andy knew the genus and how well he recognized even problem species in the field. This experience, though personally amusing, is significant. Andy has hosted a great number of bryologists, in the herbarium and in the field, and he has made good use of the opportunity. He studied *Plagiothecium* and *Isopterygium* before Bob Ireland visited there, and he learned everything he could about the Polytrichaceae from Gary Smith, the Mniaceae from Timo Koponen, and *Racomitrium* from Elva Lawton. He knows *Sphagnum* very well. I would like to think that he learned from me and Dick Andrus, just as we learned from him.

Lewis Edward Anderson, known to his wife as Lewis, to many of his friends as Andy, was born on June 16, 1912 at Batesville, Mississippi, or more precisely at the Independence community now represented merely by a store. He was the son of William Carlton Anderson and Bessie May Hawkins. His father operated a general store, known then as the Nervena Store, now as the Joe Hawkins Store (Joe Hawkins being an uncle). His father died when Andy was a young boy. His mother later married R. W. Milam, after Andy had left home. (Mr. Milam wrote and asked Andy's permission to marry his mother.) Andy attended the local Independence School and Pope High School and entered Mississippi State College at the age of 16, where he was in the Reserve Officer Training Corps. He

Student-teacher interactions at Highlands, 1979.

graduated, with a Bachelor of Science degree in botany in 1931 and went on for graduate work in botany at Duke University. He served as assistant in botany in 1931–33. He received a Master of Arts degree in 1933. He was greatly influenced by H. L. Blomquist, who was interested in North Carolina bryophytes and especially in the genus *Sphagnum*. It was while Andy was at Duke as a graduate student that he became acquainted with A. J. Sharp, who for the past 50 years has been a frequent visitor to Durham and the Andersons. Andy completed a Doctor of Philosophy degree at the University of Pennsylvania in 1936. He held a Morris Fellowship in 1933–35 and served as assistant

instructor at Penn 1935–36. His doctoral dissertation concerned the mitochondria of higher plant cells; he worked under Conway Zirkle. During this period of the Great Depression, being relatively rich owing to a fellowship, Andy was able to take full advantage of the cultural events in nearby New York City, including concerts, plays, and opera. He saw the original production of *Porgy and Bess*, for one example. He also came into contact with bryologists of the Philadelphia area, including George Kaiser, Rodney True, and Edwin B. Bartram. (Later he arranged for the purchase of the Bartram library for use at Duke University. He and Pat visited Mrs. Bartram at least once after Mr. Bartram's death.) He visited The New York Botanical Garden (and found Mrs. Britton a female Ichabod Crane).

After finishing his Ph.D., Andy spent a summer at the University of Wisconsin and then returned to Duke University where he has been ever since, except for a period of military service in 1942–45. He served as Instructor, 1936–42; Assistant Professor, 1942–47; Associate Professor, 1947–53; and Professor, 1954 until retirement in 1982. During the Second World War he served in the Pacific area on the aircraft carrier *U.S.S. Hancock*; he retired from active service at the rank of Lieutenant Commander.

In 1941 he married Ruth (Pat) Geckler of Waynesboro, Ohio. Pat had been a student at Ohio State University (and had botany taught by the Ohio State Method). She was trained as a nurse, and it was in that capacity that Andy met her while he was in the Duke Hospital with appendicitis. Pat wrote me early in 1982: "Since Philip informs us he is now 40, we realize it has been 41 years since we made the trip downtown to pick out the wedding ring. Fortunately it was a simple, not too expensive one for when the groom-to-be glanced into his billfold, there was nary a bill to be seen, and I paid for the ring. He's informed a few that he married me for my money—a bank account of $444.00, but on more truthful days he admitted that it was because of the laundry which popped his shirt buttons, mismatched his socks, and starched his shorts. No 41 years of boredom; I rather doubt any two days have been alike."

When I first knew Andy, I found him so gregarious, so jolly, so uninhibited that I visualized that he was married to a chorus girl at the very least, as did my wife when she met Andy many years later. As it turned out, Andy's mother feared the same, or worse. Actually Pat is not like that at all. She is a comfortable person, calm, efficient, quiet and unobtrusive, very kindly and good humored. She has a concern for people and particularly the elderly, many of whom have counted on her to be more than neighborly. She has a beautiful house, beautifully kept. She has always made me and perhaps I could say hundreds of other botanists feel welcome. Andy has often told me that I am just like his wife. I don't know why he would say such a thing, because it always served as a preface to some kind of tease, and I don't know anyone who is quite so pleased with his wife as Andy is. I think he referred to some of our more lovable weaknesses. For example, I bought Pat a print of Dürer's rabbit which she likes and which I have always wished I had kept (or at least bought two). We both love English toffee. Once I arrived with some I got at Macy's in New York. I lost a filling in my teeth while eating toffee after going to bed. The next morning Andy and I left for Florida. We just got out of town when he realized that he had left his wallet behind. When we got back to the house Pat couldn't talk to us because of an overburden of toffee blocking communication. That is the kind of thing Andy is bound to catch one doing!

The Andersons have five children. Philip was an Air Force pilot in Vietnam and

Pat and Andy in 1977.

elsewhere and is now a commercial pilot. Sally returned to college after her children were in school and graduated at the top of her class at Old Dominion. Nancy is a teacher. Carol is a homemaker and teacher. David was in the U.S. Marine Corps in Vietnam; he has a passion for animals and rock music. He works as a curator at the Audubon Zoo, New Orleans.

The following list of publications gives testimony to the kind and quality of research output that Andy has had. He has, of course, had a meaningful impact on his fellow

Pat and Andy with children, in-laws, and grandchildren, in 1970. Top row: Roger Miller, Philip, David, Marshall Crosby, David Goodridge. Middle: Sally, Philip's wife, Judy, Carol, Nancy.

botanists, both personally and professionally. His professional involvement can be hinted at by a summary of major awards and offices.

B. S., Mississippi State University, 1931; A. M., Duke University, 1933; Ph.D., University of Pennsylvania, 1936. Employment at Duke University, 1936–82 (Instructor, (1936–42; Assistant Professor, 1942–47; Associate Professor, 1947–53; Professor, 1954–82). Lieutenant Commander, U. S. Naval Reserve, 1944–45. President, American Bryological Society, 1950–51. Foreign Fellowships Advisory Panel, Rockefeller Foundation, 1962–66. Advisory Panel, Systematic Biology, National Science Foundation, 1959–62. President, Highlands Biological Station, 1953–54. Advisory Panel, Inland Biological Stations, National Science Foundation, 1962. Advisory Panel, Facilities, National Science Foundation, 1960–64. Council Member, Oak Ridge Associated Universities (ORAU), 1965–76. Governing Board, American Institute of Biological Sciences (AIBS), 1968–74. Curator of the Moss Herbarium, American Bryological Society, 1936–81. Executive Committee, American Bryological Society, 1936–81. Associate Editor, *The Bryologist*, 1956–64. Trustee, Highlands Biological Station, 1958–71. Research Committee, Highlands Biological Station, 1958–71. Consultant, National Science Foundation, 1972–74. President, International Association of Bryologists, 1975–81. Distinguished Founders Award and Honorary Life Membership, Nordic Bryological Society, 1978. Henry Allen Gleason Award for Outstanding Publication in Botany (with Howard Crum), 1981.

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PHYLOGENETIC ASPECTS OF SPOROGENESIS IN *ARCHIDIUM*[1]

ROY CURTISS BROWN[2] AND BETTY E. LEMMON[2]

Abstract. The sporophyte of *Archidium* differs structurally and developmentally from the sporophytes of other mosses. It is the simplest known in the Musci, lacking seta, columella, annulus and calyptra. Only a few sporocytes differentiate among cells of the parenchymatous endothecium. Certain of the adjacent sterile cells degenerate and the sporocytes are contained in a chamber lined by cells that have an ultrastructure similar to lipid-secreting cells. As the capsule matures intracapsular cells degenerate leaving mature spores free in the capsule. *Archidium* spores are the largest produced by any moss. Transmission electron microscopy reveals a thick, multilayered intine not known to occur in the spore walls of any other moss. The unique layering is due to different orientations of intine microfibrils. Microtubules in similar orientation to that of the microfibrils occur in the peripheral cytoplasm during intine deposition. The only other bryophyte known to have microtubules associated with intine deposition is *Sphagnum*. An unusual feature of late sporogenesis in *Archidium* is the occurrence of free globules that are similar to globules reported during fern sporogenesis. The *Archidium* spore, however, is most like that produced by members of Subclass Bryidae. It has a hilate, proximal aperture similar to those reported for certain annual and ephemeral mosses. Ultrastructural evidence from this study supports treatment of *Archidium* in the Subclass Archidiidae.

The sporophyte of *Archidium* differs from that of all other mosses in its extreme simplicity. It consists of an unusually broad foot, a short transitional zone, and a small, cleistocarpous capsule in which a few, scattered sporocytes undergo sporogenesis. The mature spores of *Archidium*, which attain a diameter of 200–318 μm, are the largest in the Musci. The spores are unusual in that they have a thick, multi-layered intine (McClymont & Larson, 1964) not known to occur in any other moss. The spores have not thus far provided characters useful in determining relationships of *Archidium*.

Based on a careful study of sporophyte development (Snider (1975) concluded that *Archidium* differs sufficiently from the typical pattern of sporophyte development of the Bryidae to warrant treatment of the genus in a distinct order, if not in a separate subclass, of the Bryopsida. Crum and Anderson (1981) place *Archidium* in the Subclass Archidiidae of the Class Bryopsida. This treatment places special emphasis upon the sporophytic characteristics peculiar to *Archidium* rather than on the striking similarity of the *Archidium* gametophyte to certain members of the Bryidae.

As part of our ongoing study of comparative sporogenesis in the Musci we investigated *Archidium tenerrimum* Mitt. in order to determine the mechanism of sporocyte differentiation, the pattern of spore wall development, and the fate of sterile intracapsular cells during sporogenesis. In this paper we report the ultrastructural data pertinent to assessment of the phylogenetic position of this unusual moss.

Materials and methods. Archidium tenerrimum Mitt. bearing sporophytes was collected

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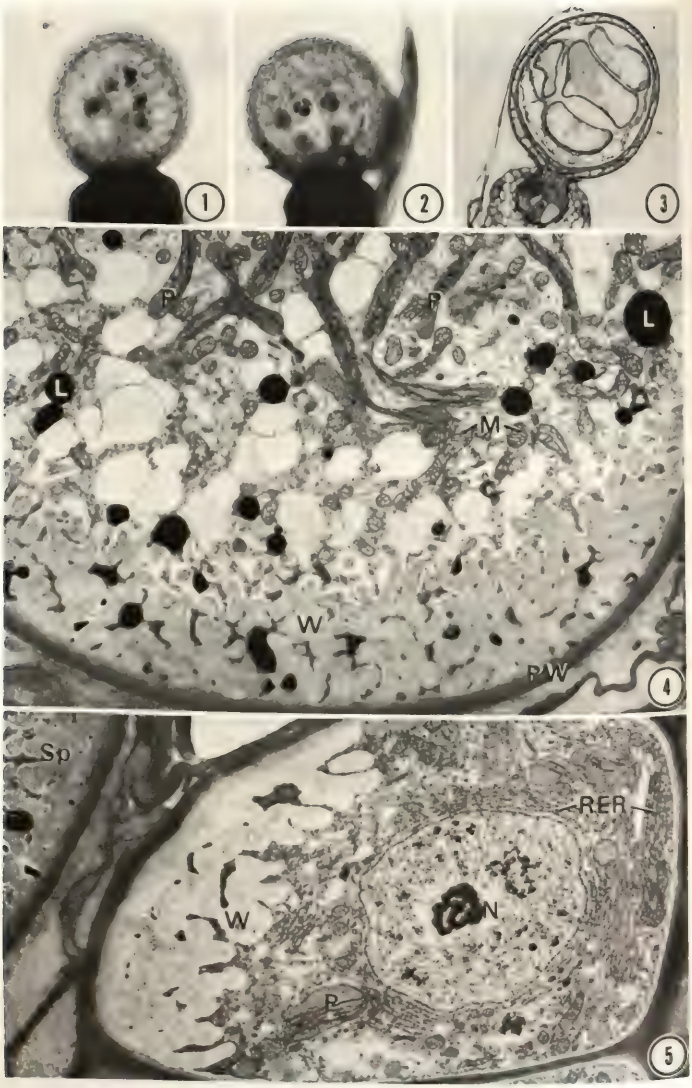
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from the same population in Vernon Parish, Louisiana, in February and December, 1981. Whole sporophytes were slit and fixed in 4% glutaraldehyde in 0.1 M Sorensen's phosphate buffer, pH 6.9, and embedded in agar. Following several washes in buffer, the material was postfixed in 2% osmium tetroxide, dehydrated in a graded acetone series and embedded in Spurr's resin. Semi-thick sections were stained with methylene blue–borax (Postek & Tucker, 1976). Thin sections were stained with uranyl acetate followed by lead citrate and studied with an Hitachi H-600 TEM.

Observations.—The Sporophyte. Unlike mosses of the Bryidae in which the capsule is nearly full size when meiosis occurs, the capsule of *Archidium* is still quite small at the time of meiosis. The average diameter of the spherical capsule at meiosis is ca. 300 μm, while the average mature capsule measures ca. 600 μm, a size comparable to that of other pygmy mosses.

Light microscope observations reveal a lack of differentiation in the sporophyte (Figs. 1–3). At no time during development is there any evidence of a seta, columella or annulus. The archegonium is ruptured unevenly by the expanding embryo and does not develop into a calyptra.

The sporophyte foot is relatively large and wide (Fig. 3). Electron microscopy shows that the foot cells at the junction with the gametophyte are differentiated into cells of the transfer type with extensive ingrowths of wall material intruding into the interior of the cell (Fig. 4). The subtending gametophyte cells likewise exhibit walls characteristic of transfer cells but the ingrowths of wall material are considerably less extensive (Fig. 5). The foot cells differ strikingly from the adjacent gametophyte cells in ultrastructure and relative proportion of organelles. The plastids of the foot cells are long, slender, and contain thylacoid membranes with reduced grana (Fig. 4). The plastids become oriented along a vertical axis as the capsule matures. In contrast, the plastids of the gametophyte, which are scattered in the cytoplasm, are more reduced with less extensive thylacoid membranes. Plastids of the gametophyte are generally ovoid in shape and frequently contain vesicles (Fig. 5). The most outstanding feature of the gametophyte cells is an extensive system of rough endoplasmic reticulum (RER) (Fig. 5). Connections of the RER to the nuclear envelope have been observed. Groups of ribosomes in typical polyribosome configurations were observed when the RER was seen in face view. Numerous lipid droplets occur in the sporophyte foot region, but are absent from the gametophyte cells at the sporophyte/gametophyte junction. Lipid droplets of similar size and appearance do occur, however, farther down in the gametophyte tissue.

The Sporocyte. A few (usually 5) sporocytes are differentiated from the solid mass of endothecial cells within a capsule (Figs. 1, 6). The sporocytes appear to be scattered in

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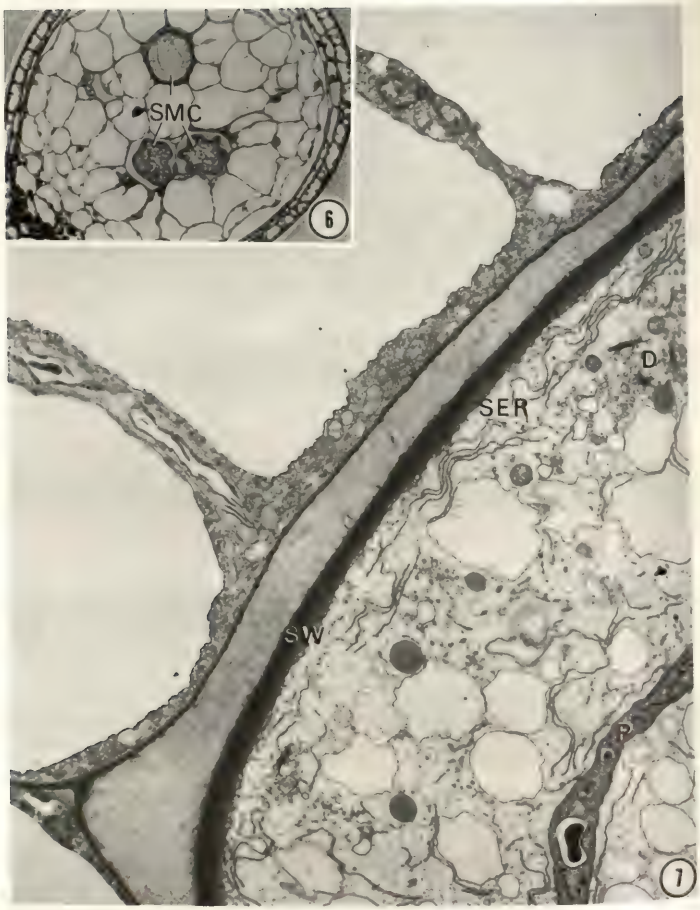
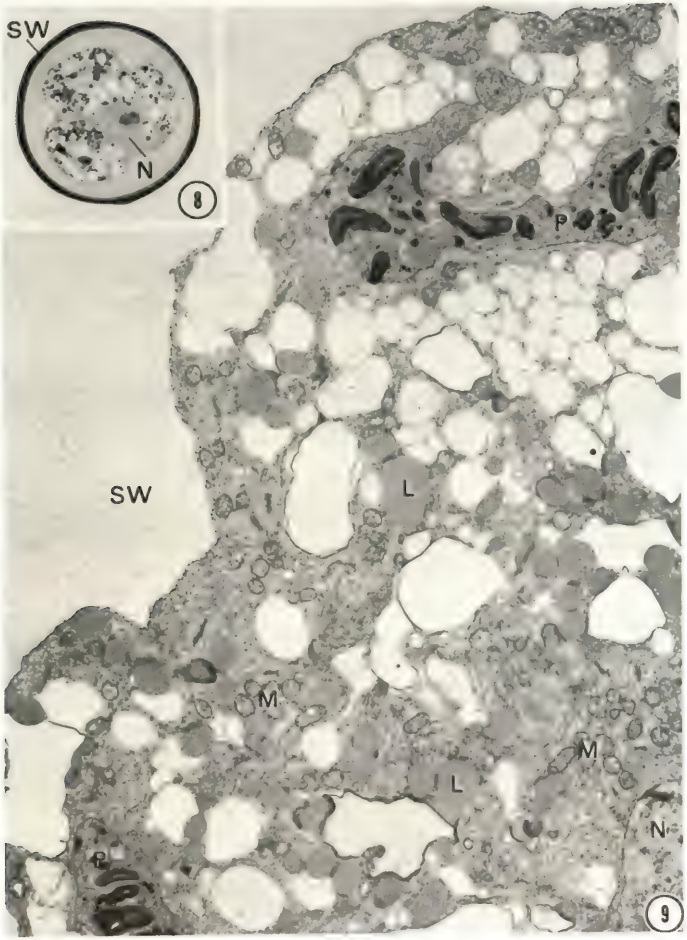
FIGURES 1–5. *Archidium tenerrimum.*—1. Optical micrograph of an unsectioned capsule fixed for electron microscopy showing differentiated sporocytes in meiotic prophase (×95).—2. Optical micrograph of an unsectioned capsule fixed for electron microscopy showing spore tetrads (×75).—3. Optical micrograph of a longitudinal section through a nearly mature sporophyte showing portions of four spores free within the capsule wall (×50).—4. Electron micrograph of a sporophyte foot cell showing wall ingrowths at junction with gametophyte cells (×6,700).—5. Electron micrograph of a gametophyte cell at the junction with sporophyte showing extensive rough endoplasmic reticulum (×6,700).

KEY TO LABELLING: AP, aperture pore; D, dictyosome; DF, distal face; E, exine; FL, foundation layer; G_1, globule 1; G_2, Globule 2; I, intine; IS, intersporal septum; L, lipid; M, mitochondrion; N, nucleus; P, plastid; PF, proximal face; Pr, perine; PW, primary wall; RER, rough endoplasmic reticulum; SMC, spore mother cell; SP, sporophyte; SW, sporocyte wall; V, vesicle.



FIGURES 6–7. Sporocyte differentiation in *Archidium tenerrimum*. See Fig. 1–5 for key to labelling.—6. Optical micrograph of capsule in longitudinal section showing early prophase sporocytes (×210).—7. Electron micrograph of a portion of a sporocyte (right of micrograph) and adjacent sterile cells (left of micrograph). The sporocyte is separated from adjacent sterile cells by two layers of wall material (×6,900).



FIGURES 8–9. Meiotic prophase in *Archidium tenerrimum*. See Fig. 1.5 for key to labelling.—8. Optical micrograph of a quadrilobed sporocyte in mid-prophase (×650).—9. Electron micrograph of the same sporocyte shown in Fig. 8. Each lobe contains a single, starch-filled plastid. Mitochondria and lipids are concentrated along the cleavage furrow between lobes (×7,300).

the interior of the endothecium. We never observed sporocytes in the outer layer of the endothecium which, according to Snider (1975), constitutes a spore sac. Each sporocyte becomes isolated from the surrounding cells by the deposition of two layers of wall material inside its primary wall (Fig. 7). The innermost of these layers is the sporocyte wall, while the material of the outermost layer becomes dispersed in the cavity in which the sporocyte undergoes sporogenesis. In early meiotic prophase the sporocyte is distinguished from the sterile intracapsular cells by its dense cytoplasm (Figs. 6–7). No plasmodesmata or cytoplasmic connections between sporocyte and surrounding cells were seen. The sporocyte cytoplasm contains numerous small vacuoles, whereas the sterile cells have large vacuoles which occupy most of the volume and restrict the cytoplasm to the perimeter of the cells (Fig. 7). The sporocyte cytoplasm has an extensive system of smooth endoplasmic reticulum (SER) in the peripheral cytoplasm where tubular SER elements are appressed to the plasma membrane (Fig. 7). Numerous dictyosomes are present in the peripheral cytoplasm associated with wall deposition in early prophase (Fig. 7). The plastids in the sporocytes are quite different from those in the sterile cells. The early sporocyte contains a single elongated plastid with dense stroma and a much reduced internal membrane system (Fig. 7). As is typical of moss sporocytes (See Brown & Lemmon, 1982), the single plastid divides twice, and the resulting four plastids become tetrahedrally arranged in the cytoplasm. Early in meiotic prophase the sporocyte becomes deeply quadrilobed (Figs. 8–9). The organelles exhibit a polar distribution with one of the four plastids at each of the distal tetrad poles and with numerous mitochondria and lipid bodies concentrated in the cleavage furrows (Figs. 8–9). The lobes will receive telophase II nuclei, and cleavage will occur along the planes established during meiotic prophase. Septa formed by vesicular fusion (Fig. 10) cleave the sporocyte cytoplasm into a spore tetrad.

The Spore. Each tetrad member (Fig. 11) shows a polarized deposition of wall material. Exine first covers the distal surface and gradually extends to the proximal surface where thin exine lamellae overlie the developing aperture (Fig. 11). Early deposition of the exine is associated with a tripartite lamella, hereafter termed the foundation layer, just outside the plasma membrane (Fig. 12). Dictyosomes in the peripheral cytoplasm are associated with vesicles containing material of appearance similar to the accumulating exine. Continued deposition of a finely granular material of medium electron opacity results in a relatively thin exine with a papillose surface (Fig. 13). Upon the papillose surface an outermost layer of perine, which consists of extremely electron dense globules, is deposited (Fig. 14). Intine is deposited uniformly inside the mature exine except on the proximal surface where a hilate aperture develops (Figs. 15–16). In the aperture area exine lamellae are interspersed with the fibrillar material of the developing pore plug (Fig. 16). The intine of *Archidium* is strikingly different from that of other mosses in that it is unusually thick and distinctly layered (Figs. 17–18). The multilayered intine is highly refractive in polarized light (Fig. 17). Underlying the developing intine is an extensive system of cytoplasmic microtubules (Fig. 19). The orientation of these microtubules is

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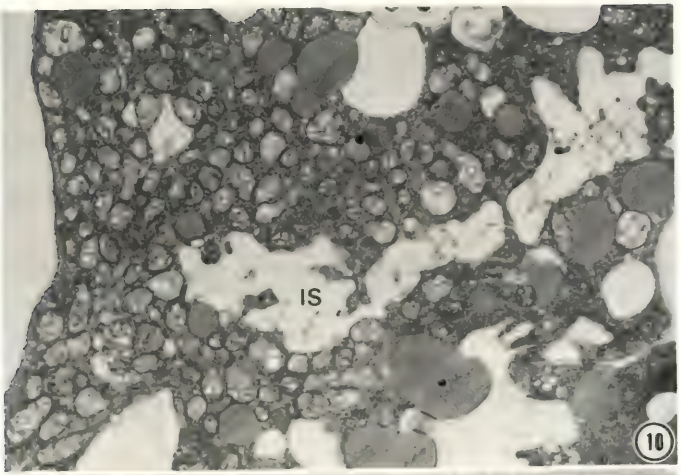
FIGURES 10–11. *Archidium tenerrimum*. See Fig. 1–5 for key to labelling.—10. Septum formation by vesicular coalescence (×11,700).—11. One member of a spore tetrad showing polarized deposition of the exine. Thin exine lamellae are associated with aperture development on the proximal face (×8,000).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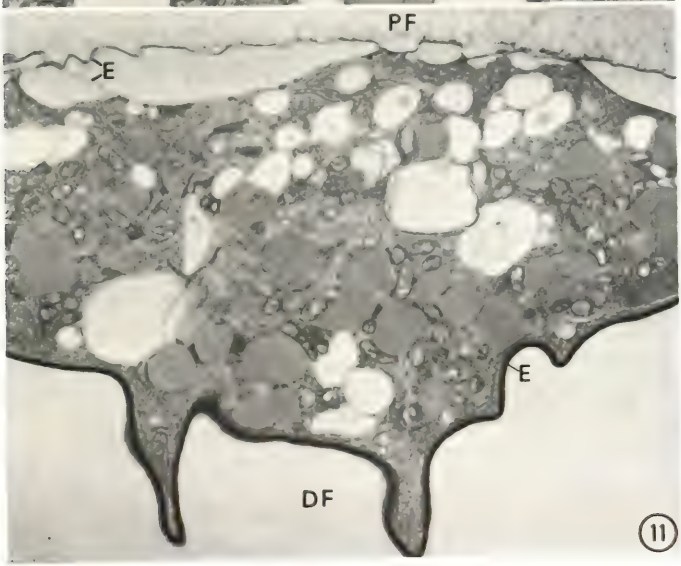
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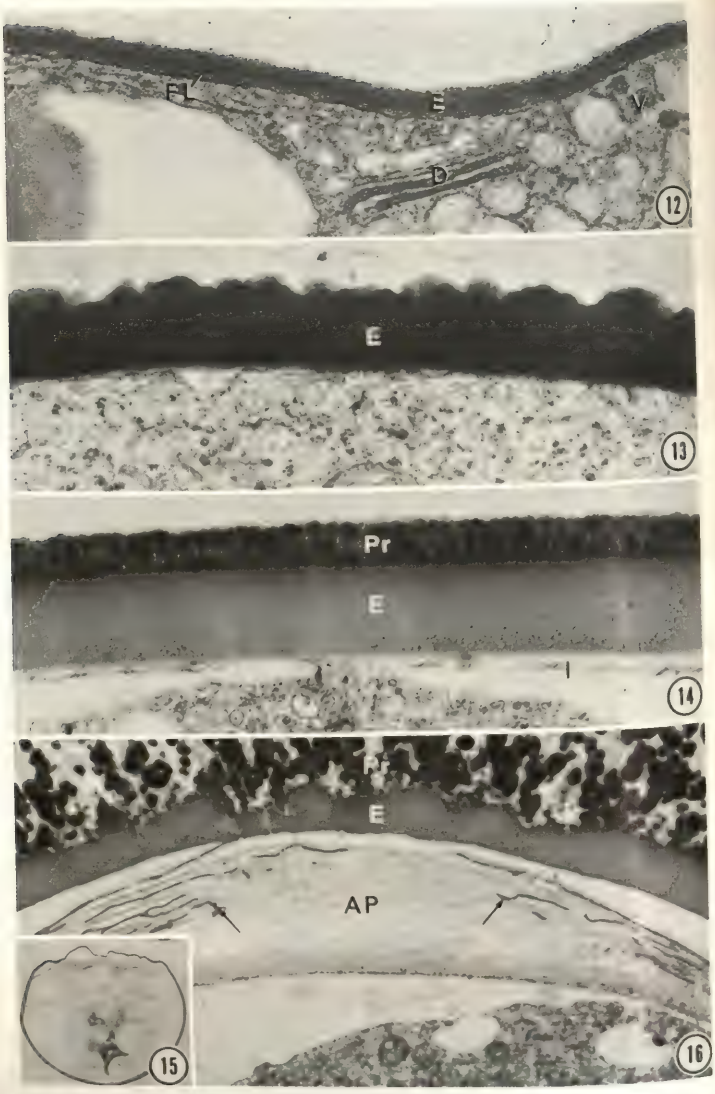
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generally similar to that of the intine microfibrils. The peripheral cytoplasm also contains numerous vesicles and a network of RER with polyribosome configurations (Fig. 19). At maturity the spore wall consists of three layers: (1) an innermost, thick, multilayered intine; (2) a relatively thin, papillose exine; and (3) an outermost, globular perine (Fig. 18).

Sterile Intracapsular Cells. The sterile intracapsular cells undergo dramatic changes during the process of spore maturation. Of special interest are the cells immediately surrounding the sporocytes (Fig. 20), which Snider (1975) termed "nutritive" cells. As the sporocyte lays down its first, outermost wall material and enters meiosis, the nutritive cells differentiate. The cytoplasm becomes localized toward the sporocyte with a large vacuole occupying the opposite end of the cell (Fig. 7). By the time meiosis is completed the nutritive cells lining the cavity around the tetrad are well-differentiated (Fig. 20). The cavity has been enlarged by degradation of certain of the sterile cells, and the remaining cells bulge into the cavity (Fig. 20). The cytoplasm of the nutritive cells is typically separated from the primary cell wall by an electron translucent space (Fig. 21) that is also visible as a clear area in semi-thick sections stained with methylene blue-borax (Fig. 20). Higher magnifications show that the nutritive cells have ultrastructural features typical of oil-secreting cells. Most obvious is the elaborate SER system with extensive tubular components (Fig. 22). The plastids are dense with little starch. The mitochondria are irregularly shaped and frequently exhibit internal cavities. Non-membrane bound, irregularly shaped globules (G_1) of medium electron opacity accumulate on the outer surface of the plasma membrane (Fig. 22). In later stages of development, distinctly different globules (G_2) appear. The G_2 are spherical, homogenous bodies that occur both within the cytoplasm and at the surface of the plasma membrane (Fig. 23). They are very similar to the spore wall exine in texture and electron opacity. G_1 globules are still present at this stage. As the capsule matures, the nutritive cells degenerate and eventually lyse, thus releasing the globules into the chamber (Fig. 24). The G_2 become coated with smaller globules of greater electron density (Fig. 24). The G_2 globules are similar in texture and opacity to the exine of spores, while the G_1 material is like the perine and outer coating of the G_2 globules.

Discussion.—The sporophyte of *Archidium* is the simplest known in the subdivision Musci. The capsule has no suggestion of the elaborate spore dispersal mechanism of true mosses, the peristome complex, and the seta is represented only by a short transition region between the spherical capsule and the unusually broad foot. Ontogeny of the *Archidium* sporophyte foot is distinct in that the foot develops directly from the lower of the two cells resulting from division of the zygote (Snider, 1975). In the Bryidae, the lower, or hypobasal, cell gives rise to the seta prior to differentiation of the foot. Despite the difference in development, the foot cells at the junction of sporophyte and gametophyte are ultrastructurally similar to those of *Funaria hygrometrica* (Bryidae) recently

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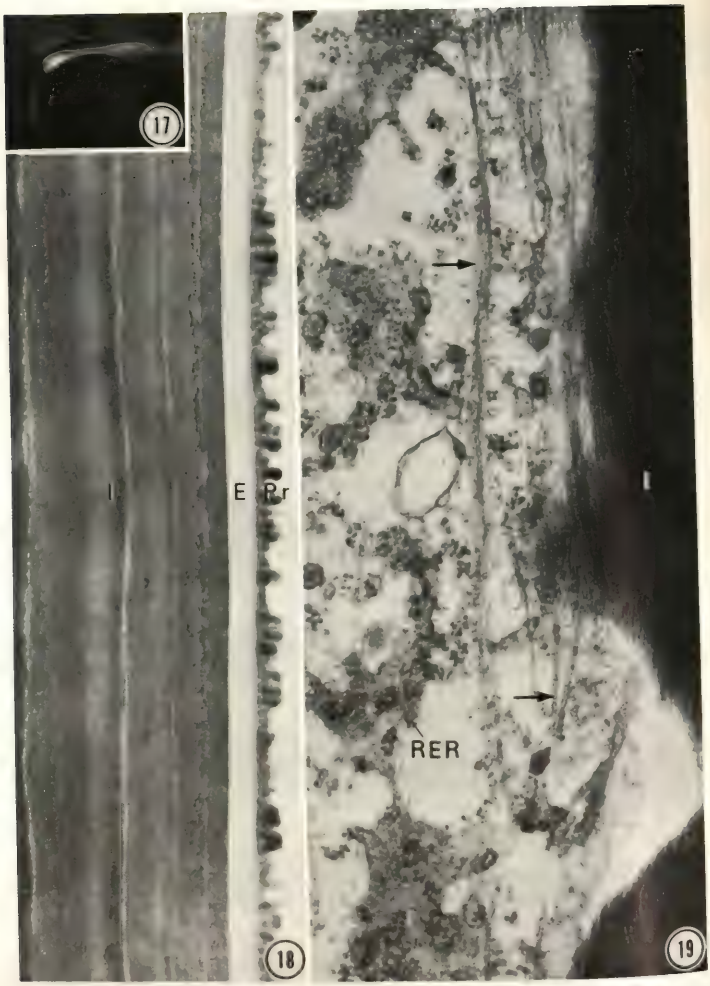
FIGURES 12–16. Stages in devlopment of the spore wall in *Archidium tenerrimum*. See Fig. 1–5 for key to labelling.—12. Early stage in exine deposition. The foundation layer appears as a white line immediately outside the plasma membrane (×75,000).—13. Nearly completed exine with papillose surface (×31,000).—14. Perine deposition on exine surface. Intine is initiated between exine and plasma membrane (×18,000).—15. Light micrograph of whole spore sectioned to show developing aperture (×260).—16. Aperture region of the proximal spore surface showing fibrillar plug outlined by splayed exine lamellae, arrows (×15,000).



FIGURES 17–19 Intine in the spore wall of *Archidium tenerrimum*. See Fig. 1–5 for key to labelling. —17. Polarized light micrograph showing refractive layers of intine (×500). —18. Portion of a nearly mature spore wall showing multi-layered intine (×17,600). —19. Microtubules (arrows) in peripheral cytoplasm during deposition of intine microfibrils (×44,700).

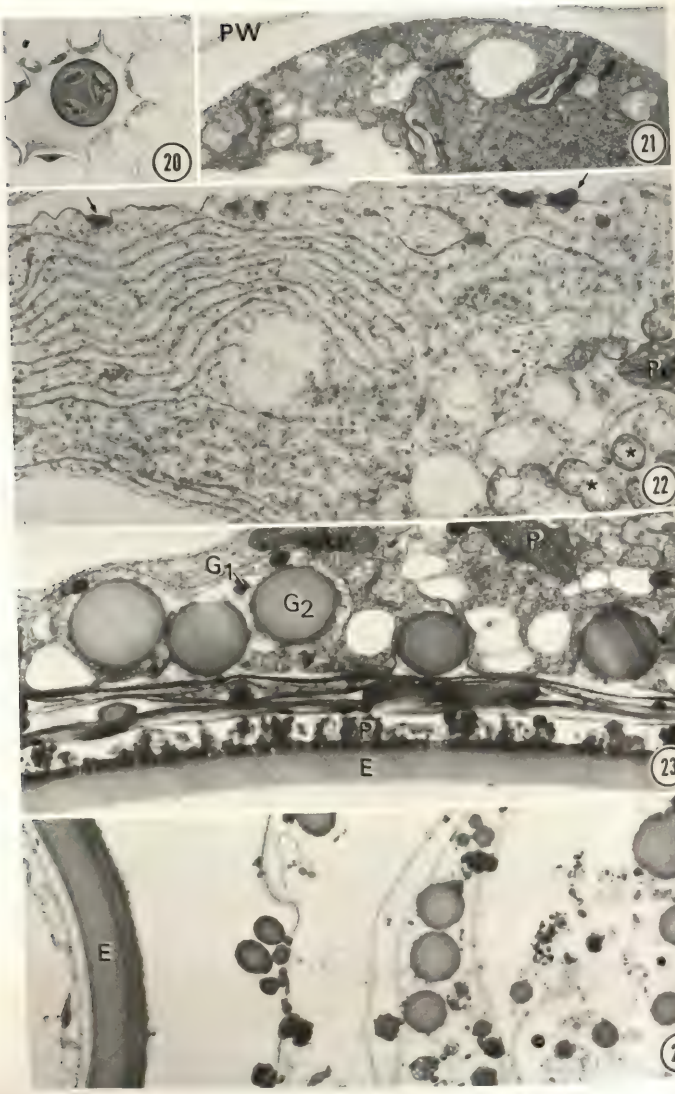
described by Browning & Gunning (1979a). Like *Funaria*, the foot cells show a type of cell architecture typical of transfer cells with highly involuted walls adjacent to the subtending gametophyte. As in *Funaria*, the foot cells are rich in mitochondria and contain numerous elongate plastids which become oriented with their long axes vertical as the capsule matures. The detailed studies of Browning and Gunning (1979b, c) have shown that the foot cells of *Funaria* sporophytes are active in the translocation of products of photosynthesis from the gametophyte.

The capsule of *Archidium* lacks the columella and spore chamber characteristic of mosses. Relatively few sporocytes, from 1–44 depending upon the species, differentiate in the parenchymatous endothecium where any of the cells within the spore sac is potentially sporogenous (Snider, 1975). The sporocytes put down a thick sporocyte wall and become isolated from surrounding sterile cells. Some of the surrounding sterile cells degenerate, and eventually the sporocytes are contained in an irregular chamber.

The sterile cells lining the spore chamber undergo a remarkable morphogenesis into what Snider (1975) called "nutritive cells," a name that suggests a supportive role in sporogenesis. The nutritive cells of *Archidium* have cytological features in common with the tapetal cells lining the spore chamber of true mosses. However, the nutritive cells of *Archidium* are all differentiated from the endothecium, whereas only the inner tapetal cells of other mosses are endothecial in origin, the outer tapetum being differentiated from the innermost layer of the amphithecium. The role of tapetal cells in mosses, has not been adequately investigated, but certain workers (Mueller, 1974; Seabury, 1975; Jensen & Hulbary, 1978) have suggested that the tapetal cells may be secretory and quite possibly are involved in synthesis of spore wall precursors.

During sporogenesis the nutritive cells of *Archidium* exhibit features that suggest secretory activity. The few dictyosomes, large mitochondria and abundant smooth endoplasmic reticulum with tubular profiles are features found to occur in secretory cells, especially those producing lipid-secretions (Schnepf, 1974). In addition, the plastids have a dense stroma and few lamellae suggesting a non-photosynthetic role. Merocrine activity in the early nutritive cells is suggested by the development of an electron translucent space between plasma membrane and the fibrillar wall. The clear area may be traversed by an occasional membrane, but is otherwise unstructured. At maturity, the nutritive cells and other sterile cells lyse. At this stage osmiophilic, homogenous globules are released. Similar bodies have been reported in fern sporogenesis where they are called "free globules" (Lugardon, 1981). As in the case of ferns, the free globules of *Archidium* may be ornamented with a coating consisting of smaller globules of greater electron opacity. These observations suggest that nutritive cells secrete first in a merocrine manner and finally become holocrine. Additional studies are needed on the process of secretion by the nutritive cells to identify the products, the method of synthesis, and the contribution of the secretions to the process of sporogenesis. Because of similarities to the process of spore formation in certain ferns, such studies could be expected to contribute not only to our knowledge of spore development in *Archidium* but also to our general understanding of ancillary cell function in spore development.

Spores of *Archidium* differ from other moss spores in their remarkably large size and the presence of an unusual multilayered intine. The much thickened intine is PAS positive, and the layered effect is heightened by a more intense reaction at the interfaces of the layers (McClymont & Larson, 1964). The intine is refractive in polarized light due to the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highly ordered microfibrils of the layers. The layers appear distinct because the microfibrils appear to "curve" in each layer and straighten at the interfaces, although, the "curved" appearance may be due to different groups of microfibrils of slightly different orientation as suggested by Schnepf et al. (1978). Microtubules in the peripheral cytoplasm are more or less parallel to microfibrils of the innermost intine. Although the association of peripheral microtubules with wall microfibrils is well documented, the precise role of microtubules in wall deposition is still not clear. Microtubules have been implicated in various aspects of wall development in moss spores. Perhaps the most striking example occurs in *Sphagnum* where a system of cytoplasmic microtubules is associated with both fibrillar intine and nonfibrillar components of the spore wall (Brown et al., 1982).

The similarity of the layered intine of *Archidium* spores to the thickened plates of peristome teeth has not escaped us. The plates are composed of stacks of microfibrils in similar orientation (Mueller, 1974; Schnepf et al., 1978). Microtubules are associated with the deposition of peristome wall material and a similar bending of microfibrils is reported. It is not known what factors might influence periodic shifts in microfibril orientation that contribute to layering of the intine, or indeed whether or not the underlying microtubules are always in parallel orientation. Schnepf et al. (1978) discuss the difficulty of actually mapping microfibrils to determine patterns of deposition. The layered intine of *Archidium* might prove to be a good experimental model for further investigation of the relationship of microtubules to microfibril orientation.

The exine of *Archidium* is generally similar to that of other moss spores. The mature exine is relatively thin with papillae contributing to surface ornamentation and is covered by globules of electron dense perine. At the base of the exine is a single tripartite strip which persists as a white line. While this foundation layer occurs in other mosses, where it is regularly seen as the first structure associated with exine deposition, it frequently disappears during later stages. The presence of the foundation layer in *Archidium* spore wall development is evidence that spore wall deposition is not strictly centripetal. Exine is deposited outside the foundation layer centrifugally while intine is deposited within the foundation layer in centripetal fashion. This pattern of spore wall ontogeny has been observed by us in *Sphagnum* (Brown et al., 1982). Although the spores of *Archidium* have certain developmental features in common with spores of both *Sphagnum* (Brown et al., 1982) and ferns (Lugardon, 1981), they are most similar to spores of the Bryidae, from which they differ principally in their large size and thick multilayered intine. The demonstration of an aperture adds an important spore characteristic that further links *Archidium* to members of the Bryidae that it closely resembles gametophytically. The hilate aperture on the proximal surface appears basically similar to apertures reported for

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FIGURES 20–24. Stages in degeneration of the nutritive cells of *Archidium tenerrimum*. See Fig. 1–5 for key to labelling—20. Optical micrograph of nutritive cells surrounding a spore tetrad (×220).—21. Electron micrograph of one of the nutritive cells shown in Fig. 20. Cytoplasm is separated from the cell wall by an electron translucent space (×8,000).—22. Nutritive cell cytoplasm showing extensive system of smooth endoplasmic reticulum, dense plastids and mitochondria with internal cavities, (×14,700).—23. Nutritive cell cytoplasm adjacent to spore wall following perine deposition. Non-membrane bound globules (G_2) appear both within and outside the nutritive cell. Plastids, mitochondria and dictyosomes are still recognizable in the relatively dense cytoplasm (×9,600).—24. Release of globules following lysis of nutritive cells. A spore is seen in the far left portion of the micrograph (×4,300).

certain annuals and spring ephemerals of the Bryidae (Brown & Lemmon, 1981). Evaluation of the evolutionary and ecological significance of the aperture in moss spores cannot be attempted until sufficient comparative information has been gathered. The occurrence of aperturate, non-green spores in *Archidium* is, nevertheless, particularly interesting in view of the fact that *Archidium* shares habitats with spring ephemeral and annual mosses. For a discussion of the ecology of *Archidium*, see the thorough treatment of Snider (1975).

Based on the ultrastructural evidence from this study, we support the treatment of *Archidium* by Crum and Anderson (1981) in the Subclass Archidiidae of the Class Bryopsida. The many important differences in structure and development of the sporophyte summarized by Snider (1975) and the additional ultrastructural evidence presented here clearly argue against the inclusion of *Archidium* in the Bryidae. *Archidium* is, nevertheless, more closely allied to the Bryidae in both gametophytic and sporophytic characters than to any other group of the Brophyta.

Moreover, ultrastructural evidence from this study supports Snider's (1975) suggestion that *Archidium* represents an early departure from the bryidean line. Any serious attempt to understand moss phylogeny must take into account the unique combination of sporophytic characters that sets *Archidium* apart from other cleistocarpous mosses which can be viewed as reductions from stegocarpous, peristomate relatives. *Archidium* has no known close relatives. The information supplied by Rushing and Snider (1980) on sporophyte development in *Lorentziella imbricata* is especially valuable in this regard as it presents evidence that *Lorentziella*, the moss bearing the closest sporophytic similarity to *Archidium*, develops in the characteristic bryidean manner rather than in the archidean manner. Lacking evidence to the contrary, we must consider the possibility that *Archidium*, as its name suggests, represents a more primitive form rather than an extreme reduction from the peristomate line.

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THE NEOVOLCANIC BELT OF MEXICO AS A BARRIER AND ROUTE OF MIGRATION FOR MOSSES[1]

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Abstract. The peculiar ecological conditions that prevail along the high elevations of the Neovolcanic Belt of Mexico have influenced moss distribution in three possible ways. First, by reduction of the floristic exchange between the valleys to the north and south of this mountain range. Second, allowing the migration of mosses from east to west and vice versa. Third, serving as a connecting floristic bridge with the main mountain systems of the country. Preliminary evaluations suggest that several species established themselves on both sides of the Neovolcanic Belt before its full development; other species have been unable to cross the mountain barrier. Alpine species have used mountain tops as stepping stones but several have not reached the eastern or western ends of the Neovolcanic Belt.

The Neovolcanic Belt of central Mexico is a mountain range located between 19° and 20° N separating the Mexican Plateau from the so-called Balsas Depression. It extends from the western to the eastern coasts and includes the highest peaks in the country. Nevado de Colima (4340 m), Nevado de Toluca (4560 m), Popocatépetl (5450 m), Iztaccíhuatl (5280 m), La Malinche (4460 m), Cofre de Perote (4090 m) and Pico de Orizaba (5650 m) are all along the Neovolcanic Belt and hardly have other altitudinal homologues elsewhere in Mexico.

In view of its generally high elevation and its volcanic nature, the Neovolcanic Belt has peculiar ecological conditions which have influenced the geographical distribution, migration and evolution of plants. At high altitudes, low atmospheric densities make the air relatively transparent to both incoming solar and outgoing terrestrial thermal radiation (Billings, 1973), and plants are thus subject to important diurnal temperature fluctuations. In addition, high ultraviolet radiation, low pressure and atmospheric composition combined with low levels of potasium, phosphorus and organic nitrogen in the volcanic substrate, are strong selective factors which prevent many plants from becoming established at higher elevations. Because of this, the Neovolcanic Belt may have served as a barrier for moss displacement from northern to southern valleys and vice versa. The same features, however, may have allowed many moss species to expand their distribution to other mountains along the range, i.e. the Neovolcanic Belt may have served as route of migration and floristic connection with other mountain chains. In this paper I will discuss

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the extent of our knowledge on the subject of the basis of previous studies and current field work in this area. The hypotheses proposed here are being tested and are part of a long-term research project.

The Barrier

Theoretically, mosses as well as other groups of plants may serve as indicators of floristic exchange between the valleys directly to the north and south of the Neovolcanic Belt. Recorded presence of a taxon on both sides of the barrier may not be, however, direct evidence of exchange between valleys. The mountains that compose this range are of Plio-Pleistocene age, while the underlying structures and adjacent regions are older (cf. Demant et al., 1976). In terms of plant distribution, this means that mosses could have migrated to present locations before the formation or full development of the Neovolcanic Belt. Mountain crossing afterwards could have been feasible, if moss species met one or more of the following conditions:

1. Have broad ecological tolerance. This, coupled with step-by-step migration, would permit mosses to cross the mountain range in a relatively short period of time. Long-term migration may lead to species differentiation and may obscure the observation of the altitudinal displacement of the flora.
2. Possess effective dispersal capacity, i.e. the ability to produce viable offspring following release, transport and establishment of reproductive structures.
3. Possess high reproductive potential.
4. Have similar habitats available for occupation on either side of the mountain barrier.

Precipitation and temperature records for several stations show that the valleys of Zacactecas to the north and the Valley of Tehuacán to the south of the Neovolcanic Belt are climatically similar (cf. García, 1973). Thus, their moss floras may be compared to determine overall similarity and evaluate the role of the Neovolcanic Belt as a barrier to the distribution of moss species between them. Unfortunately, the mosses of the Tehuacán Valley have not been investigated and there is only a preliminary list of taxa for the valleys of Zacatecas (Delgadillo & Cárdenas, 1979). The following statements are based on the continued investigation of the mosses of Zacatecas and their known distribution in the State of Puebla where the Valley of Tehuacán is located.

The latest count indicates that the moss flora of Zacatecas consists of nearly 60 species and varieties; half this number belongs to the lowland areas but only 25 are also known from Puebla. Several of the species shared by the two areas are not significant in the discussion of the Neovolcanic Belt as a barrier because they are widely distributed in Mexico and elsewhere. *Bryum argenteum* Hedw., *Funaria hygrometrica* Hedw. and *Leptobryum pyriforme* (Hedw.) Wils. are cosmopolitan, and because they inhabit disturbed sites are to be expected there regardless of geological history and age of the areas under discussion. Other species as *Aloina hamulus* (C. Müll.) Broth., *Barbula spiralis* Schimp., *Campylopus pilifer* Brid., *Funaria apiculatopilosa* Card., *F. longiseta* (Besch.) Broth., *Husnotiella revoluta* Card., *Tortula aurea* Bartr. and *Trichostomum jamaicense* (Mitt.) Jaeg. are present on either side of the Neovolcanic Belt and are suggestive of the floristic exchange that has taken place from one side to the other. Since sporophytes are

uncommon among several of these species and their distribution is relatively wide in the Americas, it seems reasonable to suppose that this has been achieved over long periods of time and that they reached their present locations even before the formation of the Neovolcanic Belt. The origin and southward or northward range extension of individual species is difficult to pinpoint, and it would be wise to defer further consideration of the matter until the phylogenetic relationships and distribution of species are better understood.

There are species in the Zacatecas moss flora that have been unable to cross the Neovolcanic Belt. Among them *Aloina rigida* var. *rigida, Jaffueliobryum arsenei* (Thér.) Thér., *Phascum cuspidatum* Hedw., *Pterygoneurum ovatum* (Hedw.) Dix., and *Ptychomitrium leibergii* Best are distributed to the north of the barrier; *A. rigida* and *P. cuspidatum* have even been reported from South America resembling in distribution the vascular plant genus *Larrea* (cf. Rzedowski & Medellín, 1958). The absence of the last named group from localities south of the Neovolcanic Belt has been explained in terms of climate (García, et al., 1960).

The Route of Migration

The peculiar ecological features of the high elevations of the Neovolcanic Belt, which were referred to in the introductory statements, and their geological history have favored the establishment of a moss flora of diverse origins. The study of the alpine flora of Mexico has shown that mosses can be grouped into five phytogeographical elements according to their overall distribution. These elements are: Northern, Meso-American, Southern, Wide-ranging and Endemic (Delgadillo, 1971). Except for a few disjunct species that have not yet been found in intermediate locations, most species in the first four elements are supposed to have arrived stepwise into Mexico following the main mountain systems in the Americas. Delgadillo (1971) has proposed that the events of migration occurred in Pliocene-Pleistocene times after the orogenic events that formed the Cordilleran System and promoted the elevation of the high mountains of Central America.

The distribution of mosses emphasizes the importance of the Neovolcanic Belt as a meeting ground and connecting floristic pathway among various American mountain systems. However, its role as a route of migration of moss species cannot be fully appreciated without detailed knowledge of the floristic similarities among the mountains included along its length. Previous exploration of Nevado de Toluca, Popocatépetl, Iztaccíhuatl and La Malinche has been incomplete and their alpine moss flora is still yeilding new records (cf. Delgadillo, 1979a). Nevertheless, published reports on this flora indicate that there is a high degree of floristic community among these four mountains. Conspicuous floristic differences include *Hymenolomopsis tolucencis* Thér. from Nevado de Toluca and *Pleuridium* spp. from Iztaccíhuatl which have not been found on the other three mountains. The absence of species from one mountain can be accounted for by incomplete exploration or relative age of the same since their ecological conditions are very similar (cf. Beaman, 1962, 1965; Rzedowski, 1978). The question is then whether there are floristic differences of importance between the eastern and western ends of the Neovolcanic Belt.

We have recently explored the alpine areas of Cofre de Perote and Pico de Orizaba on

the eastern end and Nevado de Colima on the western side of the Neovolcanic Belt. The moss flora on the eastern end is nearly the same as that found on other volcanoes; nevertheless there are several species that have remained unreported for other alpine areas. Among these are *Rhytidium rugosum* (Hedw.) Kindb., *Lepyrodon tomentosus* (Hook.) Mitt., *Morinia saitoana* Zander, Delg. & Eckel, *Bryoerythrophyllum recurvum* (Griff.) Saito, *B. bolivianum* (C. Müll.) Zander and *Trichostomum crispulum* Bruch.

The collections from Nevado de Colima are incompletely identified, but it seems that most of its alpine mosses are shared with other volcanoes of central Mexico. It is surprising, however, that several conspicuous taxa have not been discovered in this alpine area. Special search has been made in the known habitats of *Tortula* spp., *Ditrichum gracile* (Mitt.) Par., *Philonotis corticata* Crum & Griffin and *Zygodon pichinchensis* (Tayl.) Mitt., but these are apparently absent in the alpine area of Nevado de Colima.

The floristic similarity of all these mountains suggests that there has been migration of mosses from one mountain top to another and that the Neovolcanic Belt has indeed served as a route of migration for many species. The floristic differences between the eastern and western ends support the hypothesis that this floristic exchange has not been complete, i.e. that several species have been unable to reach the other end.

The history of migration of the alpine flora is a complex one. Undoubtedly, the migration of moss species has not been unidirectional as the volcanoes of central Mexico began their formation at different times (cf. Lorenzo, 1964). In addition, as I have discussed elsewhere (Delgadillo, 1979b), climatic changes have shifted downward the vegetational belts and may have strongly modified the distribution of taxa. The alpine moss flora has certainly not been indifferent to these changes.

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A QUANTITATIVE STUDY OF *THE MOSSES OF EASTERN NORTH AMERICA*[1]

DAVID M. LANE[2]

Abstract. A quantitative study of *The Mosses of Eastern North America* by Crum and Anderson (1981) provides some new information not directly apparent to users of the manual. Over 45% of the genera are represented by a single species. The overall genus to species ratio is 1:3.2. Less than 10% of the names recognized were described after the publication of Grout's (1928–1940) *Flora*. Less than 10% of the species have not been observed with sporophytes, and about the same proportion are known to possess special means of asexual reproduction. About 15% of the species have been collected solely in eastern North America. Of the nearly 100 journals cited in the bibliography, about 20 were cited more than five times. *The Bryologist* was cited much more often (over 130 times) than any of the others. The index lists over 220 names under *Hypnum*, of which only 11 are recognized as species. The pattern is similar and not unexpected in other large genera.

The publication of *The Mosses of Eastern North America* by Lewis Anderson and his colleague Howard Crum (1981) is a singular event in North American bryology. Users of the flora will find a vast wealth of information in its 1328 pages. Access to this information will be gained primarily through the keys and index for the purposes of locating descriptions and comparisons of closely related taxa. One can ask whether a broader comparison of taxa might yield further and possibly new information. The purpose of this paper is to analyze the various parts of the work in a quantitative manner to reveal any information not directly apparent from average use.

Methods. Several approaches could be taken in this analysis. A machine-readable data base could be developed by coding for each item or taxon all possible variables or characters. If the cost in labor and computer time could be justified, then correlation matrices and other statistics could be computed. Even multiple access keys and cladistic analyses could be developed. The much simpler, but still somewhat laborious, method used here involves generating frequency data for different categories by counting. Since precise placement of an individual taxon in a particular category is not always possible, consistency of application has been sought. This method is prone to human error. Quantitative comparisons, therefore, have been limited for the most part to a general discussion of frequencies, percentages, and ratios. The *G*-test was computed from a program written by the author for the VIC-20 microcomputer following the method and correction factor given by Sokal and Rohlf (1981: 745–746).

Results. Table 1 presents the results from a quantitative survey of the conspectus and a count of the number of species described in each genus. The total number of families (55) and genera (226) included in the manual represent about 63% and 28%, respectively, of the worldwide totals given in Crosby and Magill's *Dictionary* (1978). The total number

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TABLE 1. Summary of taxonomic data for each order.

ORDER	NUMBER OF			GENUS/SPECIES	MONOTYPIC GENERA	
	FAMILIES	GENERA	SPECIES	RATIO	NUMBER	PERCENT
Sphagnales	1	1	42	1:42	0	0
Andreaeales	1	1	2	1:2	0	0
Archidiales	1	1	6	1:6	0	0
Fissidentales	1	1	27	1:27	0	0
Bryoxiphiales	1	1	1	1:1	1	100
Schistostegales	1	1	1	1:1	1	100
Dicranales	4	26	89	1:3.4	11	42.3
Pottiales	3	33	70	1:2.1	12	36.4
Grimmiales	1	3	30	1:10	1	33.3
Funariales	5	13	33	1:2.5	6	46.2
Bryales	8	22	98	1:4.5	11	50.0
Isobryales	10	33	91	1:2.8	17	51.5
Hookeriales	1	5	5	1:1	5	100
Hypnobryales	13	78	203	1:2.6	39	50.0
Buxbaumiales	2	2	4	1:2	0	0
Tetraphidales	1	2	3	1:1.5	1	50.0
Polytrichales	1	3	17	1:5.7	0	0
Total	55	226	722	1:3.2	105	46.5

of species described (722) represents about 62% of the total given in the latest checklist (Crum, Steere & Anderson, 1973) for North America north of Mexico. Although the flora contains a number of large genera (*Sphagnum*, *Bryum*, etc.), many genera are represented by a single species in eastern North America. The overall genus to species ratio is only 1:3.2, and more than 45% of the genera contain only one species. Crum (1972) discussed comparable data for other plant groups and found that the genus to species ratio for mosses is among the lowest.

The bulk of information contained in Crum and Anderson's manual resides in the formal descriptions. A number of biological and taxonomic questions about mosses can be answered by comparing these data. Wyatt (1982) used this approach in his review of the population ecology of bryophytes. He found that about 53% of the mosses for which a sexual condition was given are dioicous. The results from comparisons in six different areas are shown in Table 2. By comparing the date of publication for each recognized species, it was found that only about 10% of the names were published after the time of Grout's well-known *Flora* (1928–1940). The largest proportion of these names were in the Hypnobryales.

Using the height measurements given for acrocarpous species, it appears that the majority of mosses (about 47%) are less than 1 cm high. Only a few species consistently exceed 5 cm in height. These mostly comprise the familiar genera of *Sphagnum*, *Dicranum*, *Mnium*, and *Polytrichum*. Of greater biological interest is the proportion of species possessing specialized structures for asexual reproduction: only about 12%, a figure in close agreement to those given by Crum (1972). Two of the most prominent orders, Sphagnales and Polytrichales, have no known brood bodies (propagula or gemmae); however, a large proportion of the Pottiales and Funariales do. Few species of the largest order, Hypnobryales, are described as having propagules similar to those in other orders. Perhaps the paraphyllia and pseudo-paraphyllia of this group function similarly.

Table 2. Summary of some biological data for each order and overall percentages.

Order	Since Grout	Height (cm)			Number of Species:			
		<1	1–5	>5	With Propagula	Sporophytes not known	Smooth spores	Endemic
Sphagnales	4	0	0	42	0	0 (?)	0 (?)	8
Andreaeales	0	0	2	0	0	0	2	0
Archidiales	1	4	2	0	0	0	6	3
Fissidentales	5	21	4	2	0	2	14	6
Bryoxiphiales	0	0	1	0	0	0	0	0
Schistostegales	0	1	0	0	0	0	1	0
Dicranales	4	45	37	7	9	10	32	13
Pottiales	12	67	32	0	25	30	47	11
Grimmiales	1	10	17	3	1	2	19	2
Funariales	3	25	8	0	4	0	10	3
Bryales	6	30	61	5	13	4	21	3
Isobryales	10	–	–	–	19	4	21	26
Hookeriales	0	–	–	–	1	0	3	0
Hypnobryales	20	–	–	–	15	11	48	30
Buxbaumiales	1	4	0	0	0	0	3	1
Tetraphidales	0	1	2	0	2	0	1	0
Polytrichales	0	3	10	4	0	0	16	1
Total	67	211	176	63	89	63	244	107
Percent	9.3	46.9	39.1	14.0	12.3	8.7	33.8	14.8

Less than 10% of the species have not been observed with sporophytes. Nearly half of this number are in the Pottiales, comprising nearly half of the species in the order. Almost as many species in the Pottiales are known to have specialized propagules. A third of the species in the manual have spores with smooth walls, leaving many species that might profitably be examined by the scanning electron microscope (SEM). What is not apparent from Table 2 is the striking degree of ornamentation in the genera *Pleuridium, Bruchia, Acaulon, Physcomitrium, Ephemerum, Micromitrium*, and possibly others. Many of the species in these genera have similar habitats, habits, and ephemeral life histories. The last column in Table 2 is an example of the value of floristic manuals in the quantitative analysis of geographical affinities. In this instance, about 15% of the species are endemics (i.e., taxa whose given distribution is wholly included within the broad area treated by Crum and Anderson).

Other comparisons could be made. The chromosome count data, for example, could be analyzed, but a more encompassing analysis has already been made by Anderson (1980) in his review of moss chromosome biology. It was originally hoped that During's (1979) classification of "life-strategies" might be applied. His categories are too imprecise, however, and the necessary data is lacking in the formal descriptions.

Table 3 shows the results of a simple analysis of Crum and Anderson's Bibliography. Nearly 100 different journals are cited all together. Of these only about 20 are cited more than five times. The listing in Table 3 yields few surprises. *The Bryologist* was cited much more frequently than any other journal. The other strictly bryological journals (and lichenological in some cases) are bunched closely in frequency after that. The inclusion of some journals of broader scope such as *Annales Botanici Fennici* is due primarily to the work of one or two prolific authors. It would appear from Table 3 that journals such as *Botanical Gazette* are no longer the sources of bryological literature that they once were.

TABLE 3. Journals cited five or more times in the Bibliography.

JOURNAL	NUMBER OF TIMES CITED	RANGE OF DATES	MEAN DATE
Bryologist	133	1902–1978	1962
Jour. Hattori Bot. Lab.	30	1963–1978	1971
Jour. Bryol. (incl. Trans. Brit. Bryol. Soc.)	30	1955–1978	1970
Rev. Bryol. Lichénol.	24	1888–1975	1951
Lindbergia	16	1971–1978	1974
Bull. Torrey Bot. Club	14	1889–1957	1920
Misc. Bryol. Lichen.	9	1961–1974	1970
Ann. Bot. Fenn.	8	1966–1977	1971
Hedwigia	6	1893–1941	1914
Jour. Jap. Bot.	6	1935–1976	1961
Jour. Sci. Hiroshima Univ.	6	1968–1977	1974
Canad. Jour. Bot.	6	1969–1976	1974
Bull. Jard. Bot. Natl. Belgique	6	1970–1978	1974
Bot. Gaz.	5	1879–1939	1903
Taxon	5	1973–1976	1974
Phytologia	5	1971–1976	1974

Table 4 presents data developed from the Index for the twenty largest genera by inspection. The first column lists the number of species described in the text, indicated by boldface type in the Index. The second column lists the number of other names under a given genus. The third lists the number of taxa below the rank of species whether in boldface type or not. In nearly every instance, column two exceeds column one, and sometimes column three exceeds column one also. One might ask if the numbers in each column are totally independent of each other or not. The results of a *G*-test for each pair of columns (for 19 degrees of freedom, columns one and two: $G = 187.9$, $P<<.005$; columns two and three: $G = 179.8$, $P<<.005$; and columns one and three: $G = 57.4$, $P<.005$) indicate there is some association between the number of species described, the number of synonyms listed, and the number of varieties and forms given. This suggests that there may be a common explanation for the large number of names.

There are several possibilities. In the case of *Hypnum*, for which more than 200 synonyms are listed, the explanation is historical. As Steere (1947) has pointed out, at the time of Hedwig *Hypnum* was a very large, artificial genus containing many of the pleurocarpous species then recognized. The subsequent splitting of the genus into many other, presumably more natural, genera would explain the number of species with relatively recent names alluded to previously (Table 2) in the Hypnobryales. The usual oscillation from primarily subjective lumping to subjective splitting over time, described by Lane (1979), explains in part the proliferation of names in *Sphagnum* and probably other genera. But another more important explanation is not apparent from the table. The first genus listed in Table 4, *Amblystegium*, is a good example. Crum and Anderson (p. 922) explain the inclusion of *Hygroamblystegium* and *Leptodictyum* in *Amblystegium*: "In the narrowest sense, each of these genera are recognizable and seemingly natural, but in fact, the species vary considerably and the genera shade into one another in such complicated ways that they defy rational definition." Similar problems of variability and delimitation can be found in other genera of the Amblystegiaceae, in *Sphagnum*, and in

TABLE 4. Data from the Index for twenty large genera.

GENUS	NUMBER OF SPECIES DESCRIBED	NUMBER OF SYNONYMS LISTED	NUMBER OF VARIETIES AND FORMS
Amblystegium	7	24	18
Barbula	11	30	5
Brachythecium	16	21	25
Bryum	26	102	17
Calliergon	7	7	22
Dicranum	17	51	17
Drepanocladus	7	9	23
Fissidens	27	25	21
Fontinalis	14	26	24
Grimmia	24	26	17
Gymnostomum	3	30	5
Hypnum	11	222	39
Leskea	4	54	6
Mnium	18	32	10
Orthotrichum	19	40	12
Plagiothecium	4	26	9
Pohlia	16	13	9
Polytrichum	8	20	18
Sphagnum	41	30	40
Weissia	4	33	10

Weissia (Stoneburner, 1981) to name but a few. The apparent lack of discrete taxa is analogous to a chain of islands that upon closer inspection is better described as a series of interconnected ridges and valleys. Suggested methods to resolve these problems of variability range from the often cited need for cultivation experiments to SEM study and chemosystematics to statistical analysis or, even, searching for overlapping variation within plants (Lane, 1981).

One wonders, in closing, if the mere accumulation of observational data, regardless of how experimentally or logically derived, can resolve the problem of variability as long as the main question remains a strictly taxonomic one. Eventually the question of "what should we name it?" must give way to "how and why is it so variable?". With the wealth of taxonomic information available in Crum and Anderson's manual, the work necessary to understand one of the central mysteries of bryology can proceed.

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REPRODUCTIVE BIOLOGY AND SUSCEPTIBILITY TO AIR POLLUTION IN *PLEUROZIUM SCHREBERI* (BRID.) MITT. (MUSCI) WITH PARTICULAR REFERENCE TO MANITOBA, CANADA[1]

R. E. LONGTON[2]

Abstract. *Pleurozium schreberi* sporophytes are widespread in parts of Manitoba, northwestern Ontario, northern Michigan, northern Scotland, Estonia, and Latvia. Capsule density averaged 2657 m^{-2} at five sites in southeastern Manitoba with annual spore output estimated at 100×10^6 m^{-2}, compared with capsule densities averaging only 18–352^{-2} at 12 sites in southwestern Manitoba, northeastern Manitoba and northern Scotland. Sterile shoots comprised 14% of those scored from southeastern Manitoba compared with 25–30% at the other sites. Perichaetial and perigonial shoots occurred in equal numbers in samples from southern Manitoba, but females outnumbered males by 8–10:1, and the total of male plus sterile shoots by ca. 2:1 in samples from northeastern Manitoba and northern Scotland. Shoots of each sex were shown to be aggregated within the populations. Reproductive phenology in southeastern Manitoba was similar to that in Britain, except for a delay in the spring phase of development resulting from longer winters. The low sporophyte density in northeastern Manitoba was due, in part, to sporophyte abortion. The feather moss stratum was absent from study sites up to 17 km from a smelter at Flin Flon, Manitoba. Extensive damage to *Hylocomium splendens*, *P. schreberi* and other components of the feather moss layer was recorded at sites up to 15 km from a more recently established smelter at Thompson, Manitoba. These mosses appeared to be more susceptible to pollution damage than either the woody vegetation or *Sphagnum* spp. and associated species of wet depressions. Low sporophyte density and a high proportion of sterile shoots were recorded in *P. schreberi* at sites near the edge of the area of extensive damage at Thompson, but there was no evidence that pollution had influenced the fertility of *P. schreberi* at sites > 30 km from the smelters.

The moss *Pleurozium schreberi* is generally regarded as rarely producing sporophytes in temperate parts of North America (Crum, 1972) and Europe (Allorge, 1955; Dixon, 1924; Gaume, 1956; Smith, 1978). Detailed field studies showed that fruiting populations are widespread in northern Scotland and parts of Scandinavia, but very rare throughout much of southern Britain due to a corresponding rarity of plants bearing antheridia. It was not clear whether this resulted from scarcity of male plants or failure in antheridial production (Longton & Greene, 1969a, 1979). More recently, fruiting populations of *P. schreberi* have been reported from boreal forest communities in southern Manitoba (Longton, 1976) and from the Great Lakes forests of northern Michigan (Stoneburner, 1979). The uneven distribution of fruiting populations could result either from climatic variation or from atmospheric pollution, which has historically been more prevalent in temperate parts of Europe and North America than in northern Scotland and boreal regions

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and is known to reduce the fertility of certain mosses (e.g. *Leskea polycarpa*; LeBlanc & De Sloover, 1970).

The present study was designed to investigate factors underlying geographical variation in the fertility of *P. schreberi* through quantitative assessment of sex distribution and sporophyte production in climatically different localities and at increasing distances from localized sources of atmospheric pollution in the boreal forest region of Manitoba. Coincidentally, evidence was obtained of extensive damage to the feather moss stratum dominated by *P. schreberi* and *Hylocomium splendens* at distances up to 17 km from copper, zinc, and nickel smelters. It was also planned to investigate the reproductive phenology of *P. schreberi* in the continental climate of southern Manitoba for comparison with that reported under more oceanic conditions in Great Britain by Longton and Greene (1969b).

Study Sites in Central Canada

The present observations were centered in the Province of Manitoba, west central Canada (Fig. 1). Mean air temperatures at Winnipeg in the south and Churchill in the north are 19°C and 12°C respectively for the warmest summer month and −19°C and −28°C respectively for the coldest month in winter (Scoggan, 1959). Snow cover typically persists from November to April in the south and from October to May near Churchill. Mean annual precipitation is 54 cm rainfall equivalent at Winnipeg but only 39 cm at Brandon in the south west and 41 cm at Churchill. The effects of low precipitation are offset in the north by cool summers and permafrost.

Much of the Province supports closed coniferous forest. This gives way to tundra in the north via a broad ecotone of more lightly wooded forest tundra and to aspen parkland and grassland in the dry southwest (Fig. 1). Observations on *P. schreberi* have been made in stands of *Picea glauca* on relatively dry soils, of *Pinus banksiana* on rock outcrops and in successional communities, and under *Picea mariana* both in relatively open spruce bog and in closed, mature stands. *Pleurozium schreberi* and other mosses, notably *Hylocomium splendens*, commonly predominate in an almost continuous layer of cryptogams on the ground in such forests. *Cladonia* spp. are locally abundant associates, particularly in relatively open woodland in the north, with *Sphagnum* spp. dominant in the wetter stands of *Picea mariana*. A dwarf shrub stratum, typically dominated by *Ledum groenlandicum*, occurs over the mosses in the more open stands, where the community may also include species of *Alnus, Betula, Salix*, and other tall shrubs. The shrub strata are poorly developed in the densest stands, but here a herb layer including such species as *Cornus canadensis, Linnaea borealis*, and *Moneses uniflora* may be developed. Species of *Usnea, Alectoria*, and crustose lichens are locally abundant as epiphytes on tree branches.

The fertility of *P. schreberi* was investigated throughout much of the forested region of Manitoba, particularly near Elma and Pinawa in the southeast, near Churchill, Gillam and York Factory in the north, and more centrally around Flin Flon and Thompson (Fig. 1). Observations were also made in outlying stands of *Picea glauca* in the grassland region near Brandon and at other North American and European localities. Two colonies of *P. schreberi* in southeastern Manitoba were sampled for phenological studies: the first was under *Chamaedaphne calyculata* and *Ledum groenlandicum* in an open spruce bog at

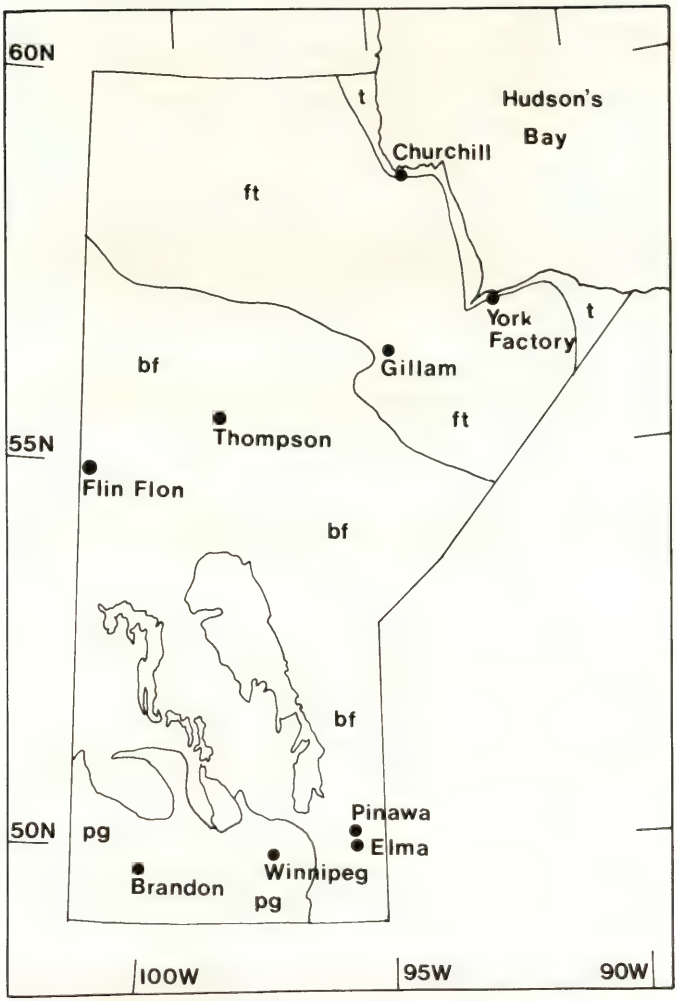

FIGURE 1. Province of Manitoba showing places mentioned in the text and the principal vegetation zones (t = tundra, ft = forest tundra, bf = boreal forest, pg = aspen parkland and grassland).

Elma, and the second was in a dense stand of *Picea glauca* and *Abies balsamea* near Pinawa.

The Impact of Smelters at Flin Flon and Thompson on the Feather Moss Stratum in Surrounding Forests

Flin Flon and Thompson are situated towards the center of the boreal forest zone in west-central Canada (Fig. 1). At Flin Flon, copper and zinc smelters have been in operation since 1930, whereas the nickel smelter at Thompson was not completed until 1961. The waste gases contain substantial amounts of SO_2 and particulates including zinc, lead, and other heavy metals. Annual discharge at Thompson is estimated at 500,000 tons of SO_2 and 10,000 tons of heavy metals (Blauel & Hocking, 1974), with SO_2 normally comprising 1–2% of the emission. The wastes are liberated through stacks ca. 250 m tall at Flin Flon and ca. 150 m tall at Thompson. The mining and refining operations form the focus for towns of approximately 8,000 (Flin Flon) and 14,000 (Thompson) inhabitants, but the smelters otherwise constitute localized sources of atmospheric pollution within extensive tracts of relatively unpolluted terrain. Their effects on surrounding vegetation have been described in unpublished Canadian Forestry Service reports. Severe forest decline, involving defoliation and eventual death of the trees was noted up to 5 km from the smelters. High concentrations of heavy metals in vegetation and soil and depletion of bryophytes and lichens were reported at greater distances, but few details of the damage to cryptogams were provided.

The present observations were made in June and July, in 1977 at Flin Flon, and in 1975 and 1977 at Thompson. Fifty-two sites between 1 km and 144 km from the smelters were examined. Most were 50–100 m from Highways 391 southwest, north and northwest of Thompson, 10 southeast of Flin Flon and 106 northwest of Flin Flon. Notes were made on the composition and apparent health of each stratum of the forest community, with particular reference to the feather mosses for which the results are summarized in Tables 1 and 2.

It can be seen from Table 1 that the feather moss layer was absent from all sites examined within 10 km northwest and 17 km southeast of the Flin Flon smelter. In contrast, *P. schreberi*, usually associated with *Hylocomium splendens, Ptilium crista-castrensis*, and *Dicranum* spp., was abundant at distances greater than 24 km from the stack. At intermediate distances, *P. schreberi* and *H. splendens* occurred in small quantity, and they were commonly yellow or brown in color except at the shoot apices.

There was evidence of an extensive, often almost continuous community dominated by *P. schreberi* and *H. splendens* at the sites near Thompson, except in wet depressions where *Sphagnum* spp. predominated. However, the feather mosses were dead or moribund at all 12 sites within 5 km north and 15 km southwest of the smelter (Table 2). At these sites there were continuous sheets of *Pleurozium* and *Hylocomium* remains, black in color, and partially covered by a layer of spruce litter. Similarly moribund remains of *Ptilium crista-castrensis* and *Dicranum* spp. were recorded in smaller quantity. At several sites the feather mosses were almost completely blackened in open areas within the forest but apparently healthy in sheltered situations (Fig. 4), for example under dense *Ledum groenlandicum*, around tree bases, or in the lee of roadside banks. In some cases *H.*

TABLE 1. Variation in the health, abundance and sporophyte production of feather mosses with distance from the smelter at Flin Flon, Manitoba, in 1977. The observations NW of Flin Flon extended into Saskatchewan.

Site	Distance (km) and direction from smelter	Dominant tree(s)[a]	Feather moss cover[b]	Feather Moss Community		Condition of feather mosses
				Dominant species[a]	Occurrence of *P. schreberi* sporophytes	
1	1NE	P.BAL	0	–	–	–
2	3NE	PM	0	–	–	–
3	5NW	PM	0	–	–	–
4	10NW	PM,PB	0	–	–	–
5	14NW	PM	1	PS	–	Yellow-brown in color.
6	16NW	BP,PB,PM	2	PS	+	Yellow in color.
7	24NW	PB	3	PS	+	Healthy.
8	29NW	PB,PM	2	PS	+	Healthy.
9	33NW	PM,PB,PT	4	PS	+	Healthy.
10	39NW	PB	5	PS	+	Healthy.
11	5SE	PM	0	–	–	–
12	9SE	PG,PT	0	–	–	–
13	11SE	PM	0	–	–	–
14	17SE	PB	0	–	–	–
15	19SE	PG,PT	1	HS,PS	–	Largely brown in color, though green at shoot apices.
16	20SE	PM	0	–	–	–
17	21SE	PM	1	PS	+	Brown and moribund in places.
18	22SE	PM	1	PS	–	Healthy.
19	27SE	PM	3	PS	+	Largely healthy.
20	33SE	PM	4	HS,PS	+	Healthy.
21	36SE	PM	5	PS	+	Healthy.
22	44SE	PM	5	PS	+	Healthy.
23	50SE	PM	5	PS	+	Healthy.
24	61SE	PM,PB,PT	4	HS,PS	+	Healthy.
25	99SE	PB	5	HS	–[c]	Healthy.

[a]BP = *Betula papyrifera*.
HS = *Hylocomium splendens*.
P.BAL = *Populua balsamifera*, as tall shrubs.
PB = *Pinus banksiana*.
PG = *Picea glauca*.
PM = *Picea mariana*
PS = *Pleurozium schreberi*.
PT = *Populus tremuloides*.

[b]0 = absent, 1 = cover < 5%, 2 = cover 6–25%, 3 = cover 26 –50%, 4 – cover 51–75%, 5 = cover > 76%.

[c]*P. schreberi* not recorded.

splendens appeared to be in a worse condition than *P. schreberi*, the former being black in color while the latter was yellow. Partial recovery of *P. schreberi* by production of short green shoots as branches of blackened, older shoots was noted in places. At site 27 (Table 3) such recovery was recorded in 1977 but not in 1975. Mosses such as *Aulacomnium palustre, Dicranum undulatum, Tomenthypnum nitens* and species of *Sphagnum*, growing in wetter parts of the forest, were apparently healthy at some sites where feather mosses in the drier areas were dead (e.g. sites 37 and 38).

Ptilidium ciliare and small acrocarpous mosses were locally frequent as colonizers of spruce litter over the dead or moribund remains of the pleurocarps at some sites near

TABLE 2. Variation in the health, abundance and sporophyte poduction of feather mosses with distance from the smelter at Thompson, Manitoba. Footnotes as in Table 1.

Site	Date	Distance (km) and direction from smelter	Dominant tree(s)	Feather moss cover[b]	Feather moss community: Dominant species[a]	Feather moss community: Occurrence of *P. schreberi* sporophytes	Condition of feather mosses
26	1975	1N	PM	3	PS	–	Moribund.
27	1975/77	4N	PM	4	PS	–	Moribund, some recovery in 1977.
28	1977	5N	PM	4	HS,PS	–	Moribund, some recovery.
29	1975/77	8N	PM	2	PS	+	Largely healthy.
30	1975/77	8N	PM	5	HS,PS	+	Healthy.
31	1975	9N	PM	5	HS	–[c]	ca.50% moribund.
32	1975	22NW	PM	4	HS	+	Healthy.
33	1975	38NW	PM	5	HS,PS	+	Healthy.
34	1975/77	1W	PM	5	HS,PS	–	Largely moribund.
35	1975/77	3SW	PM	5	HS,PS	–	Moribund.
36	1975	3SW	PM	4	HS,PS	–	Largely moribund.
37	1975/77	4SW	PM	4	HS,PS	–	Largely moribund.
38	1975/77	7SW	PM	5	HS,PS	–	Largely moribund.
39	1977	10SW	PB,PM	5	HS,PS	–	Largely moribund.
40	1975	12SW	PM	5	HS,PS	+	Largely moribund.
41	1977	14SW	PM	5	HS,PS	–	Largely moribund.
42	1975	15SW	PB,PT	4	HS,PS	–	Largely moribund; some recovery in *P. schreberi*.
43	1977	17SW	PM	4	PS	+	Moribund in open areas; healthy under dense shrub cover.
44	1977	19SW	PB	3	HS,PS	+	Largely healthy.
45	1975/77	20SW	PB,PT	5	HS,PS	+	Healthy.
46	1975/77	27SW	PM	5	HS,PS	+	Healthy.
47	1977	38SW	PM	5	HS,PS	+	Healthy.
48	1975	44SW	PM	4	PS	+	Largely healthy.
49	1977	57SW	PM	5	HS,PS	+	Healthy.
50	1975/77	68SW	PM	5	HS	+	Healthy.
51	1975	92SW	PM	3	HS,PS	+	Healthy.
52	1977	144SW	PM	4	PS	+	Healthy.

Thompson. The principal mosses were *Ceratodon purpureus*, *Leptobryum pyriforme*, and *Pohlia nutans*, all of which were recorded in fruit within 5 km of the smelter. These same mosses, together with a non-fruiting species of *Bryum*, were also locally abundant in some forest stands at present lacking feather mosses near Flin Flon, but the ground surface at such sites generally comprised bare soil or conifer litter.

Damage to the feather moss stratum extended considerably further from the smelters than obvious effects on the trees. At Flin Flon, little coniferous forest remains within 5 km southeast and 3 km northwest of the smelter, and many of the larger trees of *Picea marina* have fallen at sites 2, 3 and 11 (Table 2). Local chlorosis of tree and shrub foliage, possibly pollution-induced, was recorded at greater distances. The tree and shrub strata were intact at all the Thompson sites examined, although chlorosis was evident up to 5 km

TABLE 3. Presence or absence of *Pleurozium schreberi* sporophytes at sites in North America and Europe. *P. schreberi* was abundant at each site. Negative records are based on a search of at least 15 minutes. Additional sites are considered in Tables 1, 2 and 4.

Site	Vegetation	Number of sites		
		Sporophytes recorded	No. sporophytes recorded	Total
Manitoba, Canada, S of Lat. 56°N.	Coniferous forest.	15	0	15
Manitoba, Canada, N of Lat. 56°N.	Open coniferous woodland.	6	3	9
NW Ontario, Canada.	Coniferous forest.	9	0	9
Michigan, U.S.A.	Coniferous and deciduous forest.	3	1	4
Scotland, north of Forth-Clyde Valley.	Conifer plantations and open moorland.	6	3	9
Great Britain, south of Forth-Clyde Valley.	Conifer plantations and deciduous woodland.	0	6	6
Estonia and Latvia.	Coniferous and mixed woodland, and open bog.	9	2	11
	Total	48	15	63

southwest of the smelter. Depletion of lichens, both arboreal species and *Cladonia* spp. on the ground, in general extended comparable distances to that of the feather mosses. However, *Cladonia* spp. were locally abundant at Flin Flon sites 11 and 14 (Table 1) in the absence of the latter.

DISTRIBUTION OF POPULATIONS WITH SPOROPHYTES

Data on the presence or absence of sporophytes, based on brief observations on colonies of *P. schreberi* at 63 sites, are summarized in Table 3. Sporophytes were recorded at most sites investigated in boreal forest communities in Manitoba, at boreal and Great Lakes forest sites in northwest Ontario and Michigan, and in a range of woodland communities near the Baltic coast in Estonia and Latvia. The British data support the earlier conclusion (Longton & Greene, 1969a) that sporophytes are widespread in northern Scotland but rare south of the Forth-Clyde Valley. In addition to the data in Table 3, sporophytes of *P.*

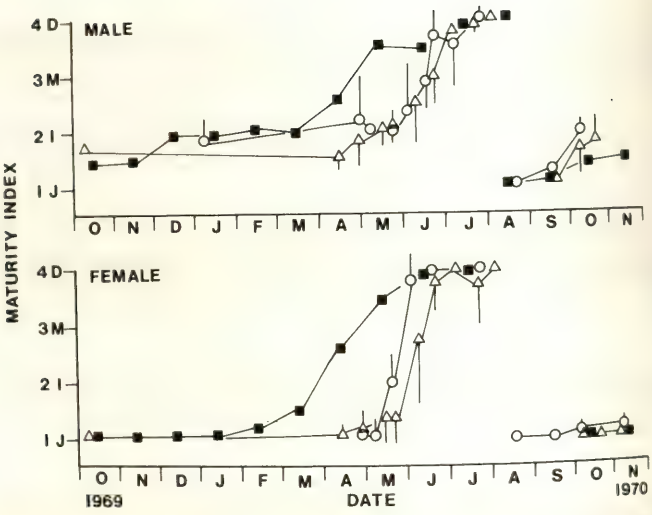

FIGURE 2. Gametangial phenology of *Pleurozium schreberi* in southeastern Manitoba showing maturity indices of samples from Elma (Δ) and Pinawa (O), compared with mean monthly indices for Great Britain (■). Vertical bars indicate one standard deviation. British data from Longton and Greene (1969b).

schreberi have been recorded by the author in montane coniferous forests in Alberta, on open rock ledges near Vancouver, British Columbia, in pine forests near Leningrad, U.S.S.R., and at many of the sites considered in Tables 1, 2, and 4.

REPRODUTIVE PHENOLOGY

Individual shoots of *P. schreberi* in Britain may produce annually up to 5 perichaetia on the main axes or up to 100 perigonia on lateral branches. The inflorescences contain on average eight archegonia or six antheridia (Longton & Greene, 1969b). Gametangia and sporophytes follow a clearly defined seasonal pattern of development. Antheridia, which were first recorded in August, overwinter in the Immature stage and dehisce during spring. Archegonia were not recorded until October: they overwinter as Juveniles but develop rapidly in spring to reach the Mature stage, at which fertilization occurs, concurrently with the antheridia. Following fertilization in spring, young sporophytes in the Swollen Venter stage were first recorded in May. Further development is generally delayed until July, but setal elongation and capsule development to the Operculum Intact stage occur rapidly during August and September. The spores are liberated between

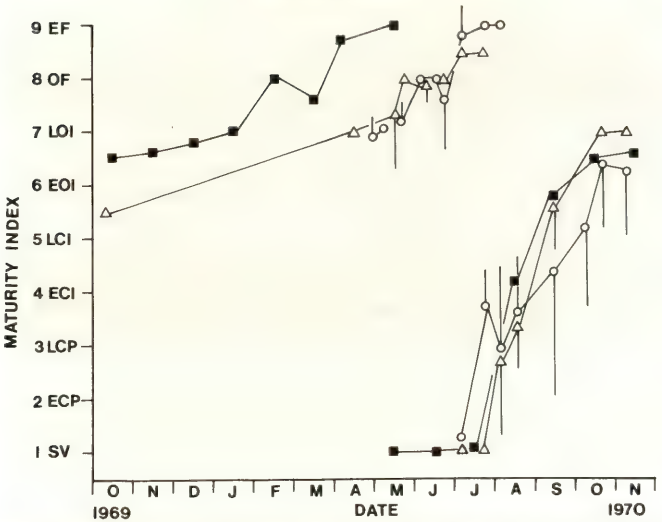

FIGURE 3. Sporophytic phenology of *Pleurozium schreberi* in southeastern Manitoba showing maturity indices of samples from Elma (Δ) and Pinawa (O), compared with mean monthly indices for Great Britain (■). Vertical bars indicate one standard deviation. British data from Longton and Greene (1969b).

January and April, approximately nine to twelve months after fertilization. Minor variation in the seasonal pattern was recorded in Britain, both between localities and between years at a given site, and examination of a limited amount of herbarium material suggested that the spring phase of gametangial and sporophytic development may be substantially delayed in parts of Canada and Scandinavia subject to prolonged winter snowcover.

The present data were obtained from samples collected at Elma and Pinawa at two-week intervals during snow-free periods from October 1969 to November 1970. All current cycle perichaetia on five female shoots, at least 10 current cycle perigonia selected from those present on five male shoots, and 10–20 sporophytes from each specimen were scored, and maturity indices calculated, using the methods described by Longton and Greene (1969b). Where developing sporophytes representing two successive annual cycles were present in a sample, separate maturity indices were calculated from 10–20 sporophytes of each cycle.

The number and arrangement of gametangia on male and female shoots were found to resemble closely the British pattern. Phenological data for the Manitoban sites are summarized in Figs. 2–3, which include for comparison mean monthly indices based on all the British specimens examined. Gametangial development began in autumn, as in Britain, but juvenile archegonia as well as antheridia were recorded as early as August at Pinawa (Fig. 2). Gametangial development in spring, and thus the period of fertilization,

were delayed by approximately three months compared with the earlier results. This delay may be related to snow cover, which persisted from November to April at the Canadian study sites in the 1969–70 winter.

Due to the delay in fertilization, young sporophytes were not recorded at Elma or Pinawa until July (Fig. 3), and it is noteworthy that there was no lag phase in the Swollen Venter stage as recorded in Britain, so that the timing of setal elongation and capsule development apparently coincides in the British and Manitoban populations. However, spore liberation, which occurs when sporophytes are in the Operculum Fallen stage, was again delayed in the Manitoba populations, where it occurred following the spring thaw, principally in May and June. It is clear from Figs. 2–3 that variation in the degree of maturation of gametangia and sporophytes within samples was greatest during periods of rapid development, as noted in *Polytrichum alpestre* (Longton, 1979).

The data in Figs. 2–3 provide little evidence of either gametangial or sporophytic development under winter snow cover. Most sporophytes in the sample collected at Elma in October 1969 were in the Late Calyptra Intact or Early Operculum Intact stages, while the Late Operculum Intact stage predominated in the first spring sample of 1970. However, it is considered probable that many capsules in the population reached the Late Operculum Intact stage before the onset of winter snow, as in both populations during 1970.

Quantitative Assessment of Sporophyte Density and Sex Ratios

Methods. Spatial density of sporophytes and sex ratios in *P. schreberi* were determined at 17 sites in relatively unpolluted parts of Manitoba and northern Scotland and at 16 sites around Thompson and Flin Flon. The localities were chosen without prior knowledge of the local fertility of the moss. All plants were stripped from ten, 25 cm square quadrats at each site and returned to the laboratory. Unbiassed sampling was ensured by positioning quadrats at intervals of 5–10 m along paced transects using a quadrat frame tossed into almost pure stands of *P. schreberi* from such a distance that any capsules present were not visible. The number of capsules in each quadrat was subsequently recorded. Sampling was carried out in 1975–77 during the months of April to July, when capsules resulting from fertilization during the year before were in the Late Operculum Intact, Operculum Fallen or Empty and Fresh stages. These are subsequently referred to as current cycle sporophytes. Capsules representing previous annual cycles were also present. It proved impracticable to distinguish in every case between those of different cycles, and thus a single total was recorded for each quadrat, comprising all sporophytes with capsules that remained attached to the parent gametophytes. Accurate counts could not be made of sporophytes resulting from fertilization during the year of observation, as setal elongation had not always occurred. In addition, a sample of 20 shoots selected at random from each quadrat was scored for the occurrence of gametangia. Each shoot was designated as male, female, or sterile, the latter being defined as lacking gametangia of any annual cycle.

Abundance of Sporophytes at Relatively Unpolluted Sites. The abundance of sporophytes proved variable between sites, and between quadrats at a given site, in the relatively unpolluted areas investigated. The highest sporophyte densities were recorded in five stands of *Picea mariana* and *Pinus banksiana* in southeastern Manitoba (Table 4).

TABLE 4. Sporophyte density and sex ratio in *Pleurozium schreberi* at relatively unpolluted sites.

Site Number	Quadrats with capsules	Capsules per quadrat			Shoots in samples		
		Min.	Mean	Max.	Male	Female	Sterile
Southeast Manitoba							
53	9	0	216.1	1067	77	85	38
54	9	0	140.3	320	46	127	27
55	9	0	47.4	104	89	93	18
56	10	3	216.5	865	77	79	44
57	10	7	210.5	578	92	95	13
Mean	9	2	166.2	587	76	96	28
Southwest Manitoba							
58	5	0	10.2	81	91	63	43
59	6	0	33.7	274	67	69	64
Mean	6	0	22.0	178	79	66	54
Northeast Manitoba							
60	4	0	1.2	5	15	141	44
61	1	0	0.2	2	11	160	29
62	6	0	3.0	13	27	117	56
63	2	0	0.8	7	11	92	97
64	1	0	0.1	1	13	114	73
Mean	3	0	1.1	6	15	125	60
Northern Scotland							
65	1	0	1.6	16	10	147	43
66	1	0	2.6	26	2	147	51
67	3	0	6.3	51	25	121	54
68	4	0	3.3	19	29	157	14
69	0	0	0.0	0	0	115	85
Mean	2	0	2.8	22	13	137	49

where capsules occurred in 47 of the 50 quadrats. The number per quadrat varied from 0 to 1067, with site means of 47 to 216. The overall mean of 166 capsules per quadrat is equivalent to 2657 capsules per m^2. It was considered that at least half the capsules represented the current annual cycle. Counts of the total number of shoots in one quadrat per site ranged from 784 to 1444 ($\bar{x}$ 1044). An average of 1000 shoots per quadrat, with approximately 50% female (Table 4), indicates an annual production of approximately 17 capsules per 200 shoots or per 100 female shoots. Haemacytometer estimates ranging from 25,000 to 255,000 ($\bar{x}$ 122,000) spores per capsule were obtained for seven capsules from site 54. Conservative estimates of 1,000 capsules per m^2 per year and 100,000 spores per capsule suggest an annual output of 100×10^6 spores per m^2 for continuous stands of *P. schreberi* at the present sites. High percentage spore germination on agar was recorded (Longton, 1976).

Sporophytes of *P. schreberi* were also present at eleven of the other twelve sites considered in Table 4, though at densities considerably less than in southeastern Manitoba. Mean number of capsules per quadrat averaged 22.0 (= 352 per m^2) at two sites in out-

TABLE 5. Sporophyte density and sex ratio in *Pleurozium schreberi* at sites near Flin Flon and Thompson.

Site Number	Date	Distance (km) and direction from smelter	Quadrats with capsules	Capsules per quadrant			Shoots in samples		
				Min.	Mean	Max.	Male	Female	Sterile
Flin Flon									
19	1977	27SE	8	0	163	647	72	106	22
20	1977	33SE	8	0	19	115	100	61	39
22	1977	44SE	9	0	39	165	79	91	30
23	1977	50SE	9	0	42	88	120	73	7
Mean			9	0	66	254	93	83	25
Thompson: sites 8–27 km from smelter									
29	1975	8N	5	0	3	28	1	38	161
30	1975	8N	8	0	22	158	15	66	119
30	1977	8N	7	0	19	49	45	44	111
32	1975	22N	5	0	24	70	32	60	108
43	1977	17SW	0	0	0	0	11	0	189
45	1975	20SW	6	0	20	45	20	75	105
46	1975	27SW	6	0	23	134	24	53	123
46	1977	27SW	2	0	1	6	6	10	184
Mean			5	0	14	61	19	43	138
Thompson: sites 38–144 km from smelter									
47	1977	38SW	10	1	104	323	58	121	21
48	1975	44SW	9	0	97	477	54	125	21
49	1977	57SW	8	0	16	68	35	67	98
50	1975	68SW	10	5	57	134	106	46	48
50	1977	68SW	10	8	121	331	54	121	25
51	1975	92SW	10	37	123	463	68	114	18
52	1977	144SW	10	2	57	252	79	82	39
Mean			10	8	82	293	65	97	39

lying stands of *Picea glauca* in the relatively dry, grassland region of southwestern Manitoba, 1.1 (=18 per m^2) in five open stands of *Picea* spp. in forest tundra near Churchill in northeastern Manitoba, and 2.8 (=45 per m^2) at five sites in stands of *Pinus sylvestris* and *Pseudotsuga douglasii* and in open *Calluna vulgaris* moorland in the Scottish Highlands. The low site means resulted from both a high frequency of quadrats lacking capsules and low densities of capsules in quadrats where they occurred.

It is clear that the numbers of capsules underestimate the occurrence of fertilization at the northeastern Manitoban sites, as setae lacking capsules were also recorded. Mean numbers per quadrat were 9.3, 8.1, 35.2, 17.0 and 15.3 ($\bar{x}$ 17.0) at sites 60–64 respectively. Many of the setae represented sporophytes that had aborted in the Early Calyptra Intact stage, as the apices were white, shrivelled, and covered by the calyptra. In other cases, the upper parts of the sporophytes were broken off so that it was not clear whether capsules had developed. In addition, substantial numbers of sporophytes that had aborted in the Swollen Venter or Calyptra in Perichaetium stages were present in the northeastern Manitoba quadrats, and a high incidence of sporophyte abortion was noted at the northern Manitoba sites considered in Table 3.

Abundance of Sporophytes Around Flin Flon and Thompson. Sporophytes of *P. schreberi* were observed at all except three of the sites near Flin Flon (Table 1) where the species occurred. The exceptions (sites 5, 15, 16, and 18) were located at the edge of the

area where *P. schreberi* was scarce or absent, and in each case feather moss cover was < 5%. Although generally absent where *P. schreberi* was moribund, sporophytes occurred at most Thompson sites more than 8 km north and 19 km southwest of the smelter. In addition, one young sporophyte in the Late Calyptra in Perichaetium stage was seen at site 43, and capsules were observed in one stand of *P. schreberi* at site 40. Sites 43 and 40 are located respectively 17 km and 12 km southwest of the smelter, considerable areas of feather moss being black and moribund in each case (Table 2).

Sporophyte density was determined from quadrats at four sites 27–40 km southeast of Flin Flon and at 12 sites 8–144 km from Thompson, observations on three of the latter being made in both 1975 and 1977 (Table 5). Capsules were present in most quadrats at the Flin Flon sites, the number per quadrat ranging from 0–647, with site means of 19–163 and an overall mean of 66 capsules per quadrat. These data suggest sporophyte densities on average rather lower than in southeastern Manitoba, but higher than in the other relatively unpolluted sites considered in Table 4. The highest sporophyte density near Flin Flon was recorded at site 19, which was the nearest to the smelter of those investigated quantitatively and the first site southeast of the smelter at which *P. schreberi* was abundant (Tables 1 and 5).

The Thompson results indicate fewer sporophytes at sites close to the area where *P. schreberi* was largely moribund than at greater distances from the smelter, in terms both of the proportion of quadrats containing capsules and mean number of capsules per quadrat (Table 5). The latter ranged from 0–24 ($\bar{x}$ 14.0) for sites located 8–22 km north or 17–27 km southwest, compared with 16–123 ($\bar{x}$ 82.1) at distances of 38–144 km southwest of the smelter. Only at site 43 were no capsules recorded: *P. schreberi* was largely moribund at site 43 (Table 2), but the quadrats were located in occasional, apparently healthy stands. It is noteworthy that there was no tendency for sporophyte density to increase with distance from the smelter in the range 38–144 km.

Sex Ratios. The numbers of male, female, and sterile shoots in the 20-shoot samples from each of ten quadrats per site are indicated in Tables 4–5. Only 14% of shoots from the five southeastern Manitoba sites were sterile. Among the remainder, females outnumbered males by ca. 1.3:1, but the excess of females occurred largely at site 54. Sterile shoots comprised 25–30% of those examined from southwestern Manitoba, northeastern Manitoba and northern Scotland. Males outnumbered females by 1.2:1 among shoots from southwestern Manitoba, and the overall sex ratio for the seven southern Manitoba sites was strikingly close to unity at 1.05 male:1 female. This result is in marked contrast to those from northeastern Manitoba and northern Scotland where the female:male ratios were 8.1:1 and 10.4:1, respectively. The number of shoots with perichaetia outnumbered the total of sterile shoots plus those with perigonia by 1.7:1 in the northeastern Manitoba smaples and by 2.2:1 for northern Scotland. No males were recorded at the single Scottish site lacking capsules.

The Flin Flon results (Table 5) resemble those for southeastern Manitoba in that only 12.5% of shoots in the five samples were sterile, and that perichaetial and perigonial shoots occurred in roughly equal numbers, i.e. 1.1 male:1 female. The results for sites 38–144 km southwest of Thompson were broadly similar, with an average of 19% sterile shoots and a ratio of 1.5 female:1 male. However, sterile shoots comprised 50% of the sample from site 49. In contrast, sites closer to the Thompson smelter showed a substantially higher proportion of sterile shoots, i.e. an average of 69%. The ratio of 2.3

TABLE 6. Numbers of quadrat-samples with various percentages of male shoots among shoots with inflorescences of either sex. Samples with 6 or more sterile shoots are excluded.

Region	0–20%	21–40%	41–60%	61–80%	81–100%
SE Manitoba	18	2	4	7	9
SW Manitoba	4	1	3	1	4
NE Manitoba	25	0	1	2	0
N Scotland	35	0	0	0	2
Flin Flon	12	2	5	3	12
Thompson	22	13	9	2	16
Total	116	18	22	15	43
Total excluding Northeast Manitoba and North Scotland	56	18	21	13	41

female:1 male was slightly greater than the average for the more distant sites, but considerably less than those recorded for northeastern Manitoba and northern Scotland.

Sex ratios in the samples from individual quadrats are summarized in Table 6, only those samples containing at least 15 fertile shoots being considered. It is evident that relatively few samples contained approximately equal numbers of males and females. In the majority, i.e. in 159 of 214 samples, one or other sex accounted for at least 80% of the fertile shoots. This bimodality is evident even when data for the predominantly female populations in northeastern Manitoba and northern Scotland are excluded, and it suggests that male and female shoots tend to occur in aggregations, rather than being evenly distributed within the populations.

DISCUSSION

The sites investigated vary in climatic and edaphic conditions, and in the composition of the forest community. All may well be subjected to some degree of atmospheric pollution. Nevertheless, the striking contrast between the abundance of *Hylocomium splendens* and *P. schreberi* in most areas studied and the absence, or moribund condition, of these mosses at sites near Flin Flon and Thompson can most reasonably be attributed to damage from the smelter emissions. The extension of the symptoms further to the southwest than to the northwest of the smelter at Thompson is in line with prevailing winds during March, April, and May. There is abundant evidence of SO_2-induced injury to mosses (e.g. LeBlanc & Rao, 1973; Nash & Nash, 1974; Syratt & Wanstall, 1969), including feather mosses (Winner & Bewley, 1978a–b). Heavy metals may also prove toxic to bryophytes at high concentrations (Rao et al., 1977), although there are many reports of mosses in polluted areas accumulating such substances to considerably above background levels without apparent damage, as in the case of lead in *P. schreberi* (Rinne & Barclay-Estrup, 1980). In view of the influence of shelter noted at Thompson, it may be significant that Gilbert (1968) reported shelter to be effective in reducing levels of SO_2, but not of smoke, around Newcastle, England. Thus SO_2 has probably been the major cause of the effects reported here, but the relative importance of SO_2 and heavy metals can not be confirmed without further study. Gilbert (1968) reported *Ceratodon purpureus* and

FIGURE 4. Moribund *Hylocomium splendens* at site 37, 4 km southwest of the smelter at Thompson, in August 1975. The same species appears healthy in the shelter of *Ledum groenlandicum* in the rear. The coin is 18 mm in diameter.

Leptobryum pyriforme, two of the locally abundant colonizers of severely polluted sites near Flin Flon and Thompson, to be particularly pollution tolerant.

The absence of feather mosses from sites near Flin Flon, compared with their presence in a dead or moribund condition near Thompson, may be a reflection of the relatively recent establishment of the Thompson smelter. The observations were made 3–5 years after the occurrence of unusually high levels of waste emission at Thompson, resulting from equipment failure in 1971–72. The moribund condition of the feather mosses at some sites could conceivably be due to these temporarily high levels rather than the cumulative effects of pollution since 1961. This possibility is supported by a partial recovery of *P. schreberi* noted in 1975 and 1977. The situation could be clarified by determining whether the recovery has been sustained. However, the observations around the older smelter at Flin Flon suggest that the feather moss stratum has been virtually eliminated over distances up to 20 km from the source, that this component of the forest community may be only partially replaced by other cryptogams, and that depletion of mosses, and also of lichens, may extend considerably beyond the limits of obvious damage to trees and shrubs. Winner and Bewley (1978a) demonstrated a comparable effect of SO_2 released from oil refineries in Alberta, with *P. schreberi* the most susceptible species, although damage to mosses does not appear to extend beyond the area of general forest destruction around a nickel smelter at Wawa, Ontario (Freedman & Hutchinson, 1980). The data from Manitoba and Alberta emphasize the necessity of containing pollutants at source if changes in boreal forest communities, through destruction over wide areas of the distinctive cryptogamic component, is to be avoided as increasing numbers of isolated industrial operations become established in northern regions. It may be noted that the current situation around Flin Flon and Thompson provides a valuable opportunity for investigating both the short- and medium-term effects on the rest of the forest community that may be set in train by elimination of the ground cryptogams, in view of their influence on permafrost, nutrient cycling, and soil moisture (Billington & Alexander, 1978, Rieley et al., 1979; Weetman, 1968).

The present phenological results support the conclusion (Longton & Greene, 1969b; Stoneburner, 1979) that the seasonal reproductive cycle of *P. schreberi* is essentially similar in Britain and North America, the differences in Figures 2–3 being largely attributable to prolonged winter snow cover in southeastern Manitoba delaying spring development. The unusually high incidence of sporophyte abortion in northeastern Manitoba may result from the even longer winters and cool summers retarding fertilization and early stages of sporophyte development to the extent that capsules fail to develop prior to the return of snow cover. The two month resting phase in the Swollen Venter stage shown by sporophytes in Britain is clearly not essential. Fertilization occurs later in southeastern Manitoba than in Britain, but is followed almost immediately by sporophyte growth so that the period of setal elongation, represented by the Early Calyptra Intact stage, coincides during July and August in the two regions (Fig. 3). Setal elongation occurred during June in greenhouse cultures of British *P. schreberi* (Longton, 1963), demonstrating that it is under environmental control.

The present survey and the report of Longton and Greene (1969a) show that sporophytes of *P. schreberi* occur widely in boreal regions and in some montane forests. *Pleurozium schreberi* reaches its greatest abundance in such areas, and thus it can hardly be regarded as generally rare in fruit (cf. Crum, 1972). There is evidence, however, that fruiting may

be decidedly rare in places both to the north (Hesselbo, 1918; Holmen & Scotter, 1971; Mårtensson, 1956), and in lowlands to the south of the boreal forest zone (Crum, 1972; Longton & Greene, 1969a). The quadrat data from southeastern Manitoba, from the sites near Flin Flon, and from those outside the region of evident pollution damage around Thompson indicate high sporophyte densities, as reported by Stoneburner (1979) from northern Michigan. The sites in northeastern Manitoba, and those in southwestern Manitoba and northern Scotland, can perhaps be regarded as lying close to the northern and southern boundaries respectively of the region of widespread sporophyte production. Spores of *P. schreberi* germinate readily on agar but have not been observed to do so in the field (Watson, 1971).

In southern Britain the extreme rarity of plants bearing antheridia could alone be responsible for the rarity of sporophytes, which were found to occur annually in occasional bisexual populations (Longton & Greene, 1969a). It is thus of interest that there was only a minor excess of females over males among fertile shoots in the quadrat-samples from those parts of Manitoba where *P. schreberi* fruits abundantly. This, again, is in agreement with Stoneburner's (1979) findings in Michigan. Conversely, females exceeded males by 8–10:1 in the samples from sparsely fruiting populations in northeastern Manitoba and northern Scotland, where a higher proportion of sterile shoots was also recorded. No close relationship was evident between sex ratio and sporophyte density in individual quadrats, except for the occurrence of low numbers of capsules in quadrats where the samples were predominantly male.

It is clear that factors other than scarcity of antheridia may limit sporophyte production in *P. schreberi*, at least locally, as at the southwestern Manitoba sites where sporophyte density was low despite an abundance of both male and female gametangia. Dry conditions may perhaps inhibit fertilization at these sites, whereas sporophyte abortion is clearly a significant factor in northeastern Manitoba. Stoneburner (1979) related variation in the abundance of *P. schreberi* sporophytes in Michigan to correlated variation in sex ratios, in the proportion of sterile shoots and in the aggregation of male and female shoots.

The conclusion that male and female plants tend to be aggregated, rather than randomly dispersed, within bisexual populations is in agreement with results for other dioecious mosses (Longton & Greene, 1967; Wyatt, 1977). This pattern is likely to result from the development of continuous colonies as a series of clones. The non-randon distribution complicates statistical treatment of the present data on sex ratios, particularly comparison of sites within each region. It may also explain occasional anomalies such as the different sex ratios recorded at site 50 in 1955 and 1957 (Table 5).

The fact that shoots with perichaetia considerably outnumbered the total of sterile shoots plus those with perigonia in the quadrat-samples from northeastern Manitoba and northern Scotland suggests that female plants outnumber males at the sites concerned. It was not possible to draw this conclusion from the earlier data for southern Britain due to the high proportion of sterile shoots (Longton & Green, 1969a). Low frequency of male plants, and a failure of some of those present to produce perigonia, were shown to contribute to the rarity of antheridia in British populations of *Plagiomnium undulatum* (Newton, 1971, 1972), and both factors could apply to *P. schreberi*.

The quadrat results from Thompson indicate low sporophyte density, and a high proportion of sterile shoots, in apparently healthy colonies of *P. schreberi* at sites within or just outside the zone of extensive pollution damage to the mosses. However, the sex

ratios at these sites were not markedly different from those in relatively unpolluted locations. Moreover, there is no indication that atmospheric pollution has reduced sporophyte density, or the proportion of fertile male shoots, at distances greater than 10 km beyond the areas of fume damage to *P. schreberi* at Thompson and absence or rarity of feather mosses at Flin Flon. Winner and Bewley (1978b) reported a decrease in sporophyte density with increasing SO_2 stress in several mosses in Alberta, including *Hylocomium splendens*, but their results for *P. schreberi* were inconclusive due to a generally low abundance of its sporophytes at their study sites. While these results do not necessarily imply that atmospheric pollution has had no influence on the fertility of *P. schreberi* in other parts of its range, they do suggest that the wide variation in sex ratio and sporophyte production between different regions is more likely to be determined by climate than by other factors. The experimental studies of Longton and Greene (1979) failed to clarify the nature of such climatic control. Further work is desirable, as relationships between sex distribution and sporophyte production, comparable with those in *P. schreberi*, are known from many other dioecious mosses (Longton 1976).

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FOSSIL EVIDENCE OF THE DISPERSAL AND ESTABLISHMENT OF MOSSES AS GAMETOPHYTE FRAGMENTS[1]

NORTON G. MILLER[2]

Abstract. Dispersed fragments of moss plants with growth that had occurred before the propagules became buried in sediment were recovered from late Pleistocene deposits at sites in central and northeastern United States. The propagules were either fragile buds or leafy segments of stems produced by irregular fragmentation of the source plants. Associated plant fossils indicate that the fragments came from two different paleoenvironments: treeless late glacial tundra and full glacial, open spruce woodland. It is concluded that wind was an important dispersal agent in the former environment, while moving water was probably significant in the latter. Dispersed vegetative propagules appear to have contributed greatly to the early establishment and spread of mosses on newly deglaciated terrain.

The importance given to vegetative propagules in the reproduction of mosses is based primarily on laboratory studies of their exceptional regenerative capacity and from the observation that certain widely distributed species either have not been found with sporophytes or produce spores only rarely. However, there is relatively little direct evidence about circumstances under which new populations of mosses become established in nature.

In arctic and alpine environments transport of fragmented bryophytes appears to be common (Miller & Ambrose, 1976). While some of the fragments can be demonstrated to be viable (*ibid.*), their actual role in establishment is uncertain. Leach (1931), in writing about the appearance of mosses on unstable soils, reported the early establishment of *Polytrichum* on bare mineral soils from plant fragments, but few other observations of this sort seem to have been made. Evidence for the dispersal of bryophyte spores comes from their representation in samples of airborne particulates (Hirst & Hurst, 1967) and in Quaternary lake sediments (e.g., Birks, 1981). Studies of establishment in nature by spores are also few.

I report here on the occurrence of vegetative propagules of mosses in Pleistocene sediments. The formation, release, dispersal, deposition, and establishment of the propagules are considered. That some of them were in the process of establishing new plants is shown by leafy branches and rhizoids and/or protonemata that had proliferated from the propagules before they were transported and buried in sediment. The probable reproductive role of such plant fragments is evaluated with reference to Pleistocene environments and to the pattern of revegetation in newly deglaciated regions.

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Methods. Sediments of late Pleistocene age at the following localities produced the fossils upon which this paper is based.

(1) Columbia Bridge, Essex County, Vermont (44° 50′ 50″ N. Lat., 70° 38′ 30″ W. Long.). Samples of organic-rich, late glacial clays, silts, and sands, collected in January 1978 at the exposure of laminated lacustrine sediment described in Miller and Thompson (1979), were put in an 8″ diameter, 500 μm mesh sieve and washed clean of inorganic materials by a jet of tap water. The initial sample size was nearly 20,000 cc of sediment, which produced 600 cc of wet, organic residue. Under 12× magnification, the residue was divided into indentifiable components, one of which was mosses. The moss fossils were stored in 70% ethanol until they were further studied microscopically. The organic residue was derived from layers of plant materials that occurred from 1.38 to 1.74 m below the top of the deposit of laminated sediment. Wood fragments from a layer at 0.84 m and from layers between 1.52 and 1.58 m were dated at 11,390 ± 115 (WIS-919) and 11,540 ± 100 (WIS-961) ^{14}C years B.P., respectively. The sediments accumulated in a large lake that once occupied a portion of the upper Connecticut River valley.

(2) Tom Swamp, Worcester County, Massachusetts (42° 31′ 51″ N. Lat., 72° 12′ 44″ W. Long.). Tom Swamp, a large tract of wooded peatland, was probed with metal rods to determine the point of greatest depth in the ca. 250 hectare basin. Near this point, a column of sediment was obtained in segments with a Livingstone piston sampler (tube diameter = 4.7 cm). A 170 cc sample of late glacial silty clay and sand between 9.72 and 9.82 m was freed of inorganic materials by washing through a 250 μm mesh sieve, and the resulting organic residue was treated as above. A sample of clay with dispersed, fine grained organics from between 9.55 and 9.65 m was dated at 12,830 ± 120 ^{14}C years B.P. (WIS-1210).

(3) Gardena section moss bed, Tazewell County, Illinois (40° 41′ 13″ N. Lat., 89° 28′ 53″ W. Long.). A 55 cc sample of Woodfordian interstadial moss peat (and associated clays and silts from the strata immediately above and below), collected at the locality described in Follmer et al. (1979: 19–24), was broken down by heating to about 80° C in a 7% solution of Na_2CO_3 for 2 hours. The compact peat was gently teased apart during this time with a glass stirring rod. The resulting slurry was poured into a 250 μm mesh sieve and washed free of inorganic sediment with tap water. The organic residue was soaked in distilled water overnight; excess water was then decanted. Further treatment and microscopic examination of the fossils were made following the procedures described previously. A sample of the moss, which occurred 2.52 m from the top of the section, was dated at 19,680 ± 460 ^{14}C years B.P. (ISGS-532; Follmer et al., 1979).

The drawings were made of images seen through a Wild M5 microscope equipped with a drawing tube.

Results. Sediments at each of the three sites contained well preserved fossil mosses, including vegetative propagules with proliferations. The composition, phytogeography, and paleoecology of the floras will be detailed elsewhere. Therefore, these matters are only summarized here.

The late glacial deposit at Columbia Bridge produced a rich and diverse bryoflora of 45 extant species of mosses, most of which are known to be calcicoles. While none is strictly arctic or subarctic in present distribution, all of the mosses have "northern" ranges, and many now occur well into arctic latitudes. Represented are species of rich fens (*Campyl-*

ium stellatum, Drepanocladus revolvens, Scorpidium turgescens), calcareous seeps (*Catoscopium nigritum, Cratoneuron commutatum, Hygrohypnum luridum, Meesia uliginosa*), moist to dry calcareous soil and/or rocks (*Bryoerythrophyllum recurvirostre, Ditrichum flexicaule, Hypnum vaucheri, H. revolutum, Thuidium abietinum, Tortella inclinata*), and somewhat acid, well drained soil or acid rock (*Polytrichum juniperinum, P. piliferum*).

The basal inorganic sediments of the Tom Swamp basin contained a similar late glacial flora, although fewer species were represented. Fossils of the following mosses were identified in the sample: *Bryum* sp., *Calliergon sarmentosum, Distichium* sp., *Ditrichum flexicaule, Drepanocladus* sp., *Hypnum revolutum, Meesia longiseta*, and *Tomenthypnum nitens*. In addition leaves of *Aulacomnium turgidum* were present in the next lower sample (9.82–9.92 m). Most of these species are calcicoles. They indicate that rich fens and/or calcareous seeps and flushes occurred on surfaces above the lake that occupied the Tom Swamp basin during late glacial time. Both *Aulacomnium turgidum* and *Calliergon sarmentosum* are arctic-alpine in their present distributions, and both are now found in eastern North America only as far south as the highest mountains in New Hampshire and New York State.

The Gardena moss bed (Miller, 1979) consisted of plants of the following species: *Bryum pseudotriquetrum, Campylium stellatum, Cinclidium stygium, Drepanocladus aduncus* s. lat., *D. revolvens, Hypnum lindbergii, Mnium medium*, and *Scorpidium turgescens*. This interstadial, full glacial flora is evidence for the existence of rich fens or some similar vegetation in which calcareous ground water was continuously present. Although *Hypnum lindbergii* and *Mnium medium* are not typical rich-fen mosses, they have been found, for example, on Bathurst Island, arctic Canada, in wet, calcareous "tundra meadows" associated with all other species represented in the moss bed except *C. stygium* (Miller & Ireland, 1978).

Vegetative propagules recovered from the three deposits are illustrated in Figure 1. The progagules were bud-like plant apices (Fig. 1a, d–e), segments of leafy stems (Fig. 1b–c), and an isolated leaf (Fig. 1f). The propagules were uniformly small (0.75–2 mm in length), although the actual size of the fossils was usually larger because of the proliferative growth. Vegetative propagules of *Scorpidium turgescens* were abundant in the Gardena moss bed sample, as were small fragments of leafy plants in both the Columbia Bridge and Tom Swamp assemblages. However, of the hundreds of fragments present in each assemblage, only those that are illustrated had proliferations.

Identification of the fragments proved difficult because they were small and abraded. Furthermore, the leaves of most proliferated branches were immature and diagnostic features were undeveloped. Whole-mount observations of microscopic detail were made, but dissections were not undertaken because of their uncertain value. The following observations pertain to the specimens.

Figure 1a. A terminal bud-like aggregation of apical leaves; costa strong, percurrent; leaves with margin of differentiated cells; upper leaf cells about three or four times longer than broad; specimen definitely a species of *Bryum*.

Figure 1b. Fragment of leafy stem, both base and apex absent; leaves abraded, costa excurrent, cells not well preserved; identity unknown.

Figure 1c. Highly degraded fragment of leafy stem; cellular details poorly preserved and obscured by adhering silts and clays; leaves of new growth mostly broken near tips;

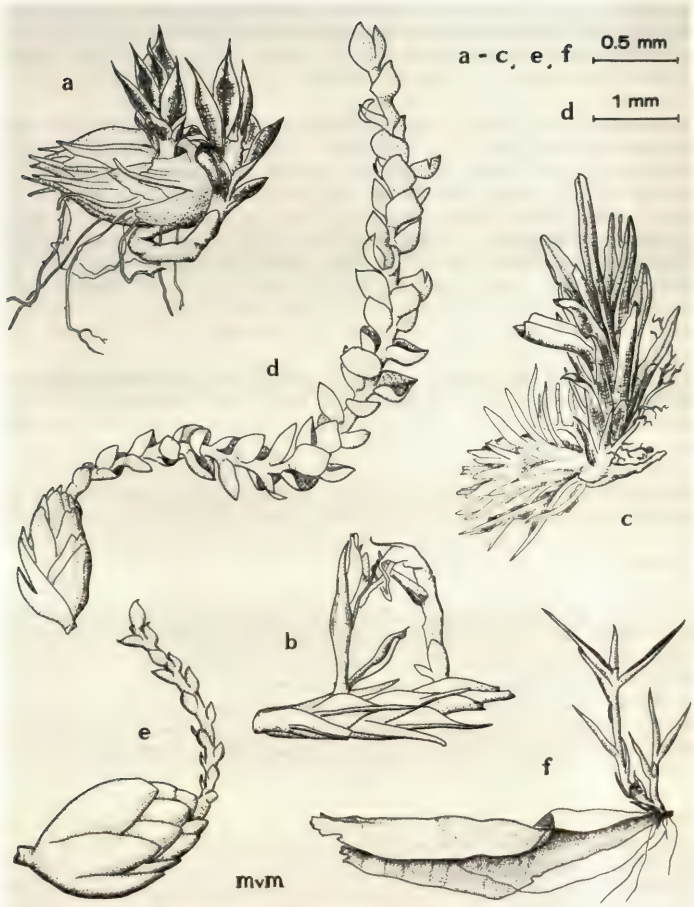

FIGURE 1. Fossils of moss propagules with proliferations. a, *Bryum* sp., bud and two stems proliferated from leaf axils (late glacial sediments, Columbia Bridge, Vermont); b, moss, leafy stem, and two stems proliferated from leaf axils (same); c, moss, eroded leafy stem, and proliferated shoot (same); d–e, *Scorpidium turgescens*, fragile buds and proliferated leafy stems (interstadial Wisconsinan, Tazewell County, Illinois); f, *Calliergon* sp., leaf and proliferated plantlets (late glacial sediments, Tom Swamp, Massachusetts).

areolation of lower parts of leaves similar to *Ceratodon purpureus*; identification tentative because the characteristic toothed apices of that moss could not be demonstrated clearly.

Figure 1d–e. Bud-like aggregations of apical leaves, these often poorly preserved; new growth showing more or less clasping leaf bases and leaf apiculi; fossils identical to herbarium specimens of similar modern material of *Scorpidium turgescens*.

Figure 1f. Leaf, basal parts mostly absent, although some larger, thin-walled cells present at one corner; costa strong, extending two-thirds the length of the leaf; two plantlets proliferated from a position just below the leaf apex; leaf in general poorly preserved, but similar to those of some species of *Calliergon*. Correns (1899: 318), for example, illustrated a plantlet and rhizoids at the apex of a leaf of *Calliergon stramineum*.

Several patterns were apparent in the mode of proliferation in the fossils: 1) new branches from leaf axil(s) of the progagules, rhizoids and/or protonemata often present (Fig. 1a, c); 2) new axillary branches only (Fig. 1b); 3) resumption of terminal growth of the stem (Fig. 1d–e); and 4) new plantlets and associated rhizoids and/or protonemata from cells of a leaf (Fig. 1f).

Discussion. The fossil plant fragments are interpreted as propagules for the following reasons: 1) their shapes and small sizes, which indicate their suitability for dispersal; 2) presence of proliferations that must have grown before the fragments were deposited and buried in sediment; and 3) recovery of the propagules (at least in the case of the Columbia Bridge and Tom Swamp fossils) at places distant from their points of origin (which indicates that dispersal had indeed occurred).

The propagules are of two kinds: those characteristically formed by a species, e.g. the fragile buds, "Bruchknospen," of *Scorpidium turgescens*, and those of less uniform morphology, the production of which is related to the fragmentation of the source plants. Propagules of *S. turgescens* were reported to have a role in vegetative reproduction by Correns (1899), Paul (1924), and Karczmarz (1971). Paul evaluated the potential of the fragile buds of *S. turgescens* to produce new growth and found that over 90% of the buds in two independent trials had proliferated after several weeks in Petri dish cultures. Working with samples of wind-dispersed bryophyte fragments from arctic Canada, Miller and Ambrose (1976) found that 12% of the fragments formed new growth under laboratory conditions. The propagules were obtained in the summer from a lingering snowbed, and over 4000 viable plant fragments were estimated to have occurred per cubic meter of snow.

The mechanisms by which the propagules were produced or released from the source plants cannot be determined directly. In the Arctic wind plays an important role in the fragmentation of plants (Miller & Ambrose, 1976) and in the transport of organic detritus (Teeri & Barrett, 1975). The Columbia Bridge and Tom Swamp fossil mosses were associated with the leaves, fruits, and seeds of herbs and low and high shrubs. The absence of trees indicates that late glacial landscapes near these sites were physiognomically similar to tundra. This circumstance implicates the wind as a causative agent in the fragmentation of moss plants, but other factors such as repeated freeze/thaw cycles may have been important also. Buds of *Scorpidium turgescens* are released when the plants are wet (Paul, 1924) or as they dry (Correns, 1899).

Dispersal of the fragments presumably was by wind, moving water, or a combination of both. When dry or partly dry, the buds of *Scorpidium turgescens* float, and moving water may disperse them in nature. The Gardena moss bed, which contained buds of *S.*

turgescens, accumulated at a time of spruce dominance, with pine present regionally and sedges abundant locally (King, 1979). Other late Pleistocene records of this moss, e.g. its presence at the Columbia Bridge site, are from landscapes that were more open, which indicates the potential role of wind in the transport of buds and other plant fragments over the surface of the ground. Several investigations undertaken in the arctic document the role of wind in moving and generating deposits of plant materials including mosses (Teeri & Barrett, 1975; Miller & Ambrose, 1976).

The processes involved in the deposition of propagules depend on whether they are being moved by wind or by water. Floating buds of the aquatic moss, *Scorpidium turgescens*, may lodge at new sites among plants or other objects or become stranded with changes in water depth. Wind- or water-propelled fragments of terrestrial mosses, particularly those with divergent leaves, may be stopped by plants or other objects. Those transported over the surface of the ground accumulate on lee slopes or other places where a decrease in the velocity of the wind causes deposition of airborne debris. Most of the fossil propagules reported here are from terrestrial mosses. The proliferations of these are oriented perpendicularly to the long axes of the propagules, indicating that the propagules had started to grow on horizontal surfaces before being dislodged and transported to the sediment traps from which they were recovered as fossils. The propagules are evidence, therefore, of the initial phase of establishment of new plants from dispersed vegetative fragments.

The rapid appearance of mosses on soils exposed by the melting of glacier ice has been documented by several studies of plant immigration in areas of active deglaciation. In the Omnsbreen glacier region of Norway, for example, the first group of pioneer mosses appeared on surfaces between two and five years after the land emerged from ice (Elven, 1980). Studies in such areas, which are to some degree analogs of late glacial conditions, provide evidence of the rapidity with which certain mosses are able to colonize new sites. Elven suggested that morphological adaptations to dispersal by wind or other agents were less important than the capacity to produce large numbers of diaspores. In certain environments abundant moss propagules may be produced through plant fragmentation. For some species, it seems likely that such vegetative propagules provided the means for recolonization of newly deglaciated areas during the Quaternary. In line with this reasoning Willson (1981: 288), in a review of the ecological implications of plant life cycles, concluded that "asexual reproduction is probably adaptive in colonizing and exploiting ephemeral, patchy resources." In the context of the paleoenvironments discussed here, reproduction by vegetative propagules supports this view. In mosses the relationship between reproduction by plant fragments and spores might be further explored by studies in areas where the revegetation of freshly exposed surfaces can be followed through time.

The fossil propagules, considered in conjunction with studies of the dispersal of fragmented moss plants over treeless landscapes by wind, indicate the importance of vegetative reproduction in the establishment of mosses on surfaces newly freed from glacier ice. The process of vegetative reproduction helps to explain the rapid appearance of a diverse bryoflora in eastern and central North America during late Pleistocene deglaciation, although the part played by spores in the establishment of new populations during this time remains to be assessed. Dispersal of vegetative fragments in arctic and alpine environments may also help to explain certain anomalous distribution patterns. The role of vegetative propagules of mosses in the revegetation of glaciated regions is likely to become more fully documented as Quaternary paleobotanical studies continue.

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Addendum

Stratigraphic studies of Holocene peats I completed since the preceding was written have produced an additional occurrence of a fossil moss bearing proliferations (Fig. 2). While the specimen is poorly preserved and new, predepositional growth involved only juvenile leaves, the shape, placement, and areolation of both adult and juvenile leaves indicate that the fossil is almost certainly part of a plant of *Ceratodon purpureus* (Hedw.) Brid.

The fossil moss is from Gleason Bog, Cheboygan County, Michigan (45°33′56″ N. Lat., 84°42′18″ W. Long.), a 0.34 hectare basin now occupied by a *Chamaedaphne-Sphagnum* heath and surrounded by sandy uplands of low relief. The basin lies below the Glacial Lake Algonquin shoreline and is about 2.5 km west of the University of Michigan Biological Station. The fossil occurred in a 47 cc sample of peat taken from a depth of 140–155 cm. The age of this peat is unknown, but that between 191 and 196 cm had a radiocarbon age of 7670 ± 90 ^{14}C years B.P. (Beta-6458), and peat higher in the section (95–100 cm) was dated at 4500 ± 110 ^{14}C years B.P. (Beta-6457).

Plant fossils associated with the moss help to specify the nature of the paleoenvironment at and near the basin at the time the moss fragment was deposited. Pollen analysis of sediments between 140 and 160 cm revealed a high pine component (70–80%) and low oak, elm, and birch values (total = 15%). Hemlock percentages were very low (0.2–2%),

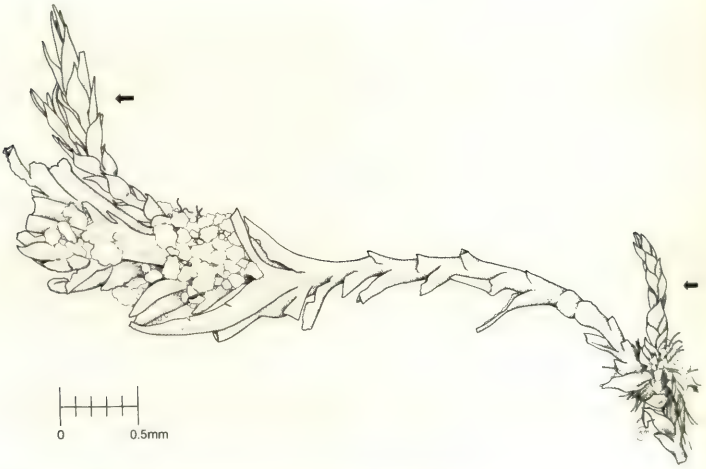

FIGURE 2. Fossil of *Ceratodon purpureus* from Gleason Bog, Michigan, showing proliferations (at arrows).

but needle fragments of hemlock indicated its presence near the basin. Macrofossils of aquatic plants (*Brasenia schreberi, Potamogeton* sp.) and fen species (*Cladium mariscoides, Dulichium arundinaceum*) establish that open, shallow water had occupied the basin early in its history. These data show that the vegetation of the dry, upland soils adjacent to the basin was a pine-dominated forest with an admixture of oak and birch, while that in the basin was a circum-neutral or slightly alkaline fen wetland. The existence of openings in the forest vegetation near the basin is indicated by the frequent recovery of achenes of *Potentilla norvegica* from the peat between 150 and 196 cm. Because *Ceratodon purpureus* now grows in forests near Gleason Bog, the fossil perhaps originated from plants so established in the past.

As discussed earlier in this paper, the proliferated moss propagules from the Columbia Bridge, Tom Swamp, and Gardena sites were deposited in either open, more or less treeless landscapes or in spruce woodland. The Gleason Bog fossil demonstrates that fragmentation, proliferation, and transport following and perhaps before proliferation can occur when upland surfaces are covered with conifer-hardwood forests of Holocene age. It is difficult to specify what dispersal agent operates under these conditions. Experiments designed to trap propagules in a variety of topographic and vegetational settings may help to decide the relative importance of surfical water flow and transport by wind.

Monogr. Syst. Bot. Missouri Bot. Gard. 11: 79–91. 1985.

SPONTANEOUS AND INDUCED MEIOTIC ABERRATION IN THE MOSS, *HOOKERIA LUCENS* (HEDW.) SM.[1]

M. E. NEWTON[2]

Abstract. Spontaneous meiotic irregularity in a specimen of *Hookeria lucens* is attributed to half-chromatid breakage and reunion resulting in anaphase-I bridges with parallel side-arms. The interpretation is substantiated by de-spiralized chromosome configurations induced by heat shock during growth, a treatment which also has the effect of reducing or suppressing synapsis and/or crossing-over and of inhibiting subsequent anaphase. Temperature induced univalent formation is therefore seen and discussed as a potential source of error in the determination of moss chromosome numbers. It is also argued that it is only in the presence of induced irregularities that sporogenesis fails completely. Significant abortion does occur in capsules affected by spontaneous aberration, but the size of 90% of the surviving spores corresponds with a normal distribution. It is suggested that the remaining 10% incorporate some chromosomal deletion or duplication.

Hookeria lucens (Hedw.) Sm., a monoecious species, is of considerable cytological interest for its irregular meiosis as much as its differing chromosome numbers. Heitz (1928), on the basis of gametopohytic mitosis, was uncertain of the number but considered it to be about $n = 12$. It has since been found in meiotic material, however, that $n = 11$ in the Caucasus (Lazarenko et al., 1967, 1971) and $n = 12$ in Britain (Smith & Newton, 1968), the latter having been confirmed mitotically by Inoue and Himeno (1977, 1978). Moreover, Smith and Newton (1968) pointed out that the kind of meiotic irregularity observed in one British specimen might be interpreted as evidence of there also being plants in which $n = 6$ or $n = 9$. The purpose of this paper, therefore, is to re-examine the facts in the light of recent work which introduces a new dimension to bryophyte cytology.

Materials and methods. A large sample bearing immature capsules was collected in cool, damp weather from deciduous woodland in Roeburndale, Wray, near Lancaster. It was maintained in humid conditions shaded from direct sunlight at a temperature of approximately 10°C. Meiosis was studied in 4 capsules, as was mitosis in 15 shoot apices. The material was then subjected to temperatures of 20–25°C for up to 3 days, heat shock during growth being known to induce chromosome de-spiralization in higher plants (cf. Darlington & La Cour, 1976). During this time, 4 further capsules were examined for meiosis. All remaining sporophytes were allowed to develop to maturity, when spore size was recorded in 25 capsules.

Cytological squash preparations were stained in propionic orcein, either using stem apices fixed overnight in 3:1, absolute alcohol:glacial acetic acid or using fresh sporophytes. The techniques have been described in detail previously (Smith & Newton, 1966; Newton, 1977). In addition to untreated material, some gametophytes were grown for two days on filter paper moistened with 0·5 Knop's inorganic nutrient solution and then subjected to six hours' treatment with 0·05% colchicine or 0·002M 8-hydroxyquinoline

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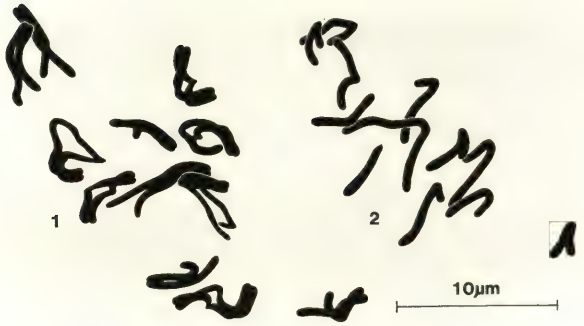
prior to fixation. Temperatures of 10°C and 18°C were employed for each of these treatments. Permanent slides have been kept, and a voucher specimen will be deposited in the School of Plant Biology, University College of North Wales, Bangor, Gwynedd, LL57 2UW.

Results. The gametophytic complement consisted of twelve chromosomes (Figs. 1–2) ranging in size from 7·5 μm down to 4·5 μm at metaphase, one of intermediate size bearing a terminal nucleolar organizer (Fig. 3). The effects of neither of the two inhibitors of micro-tubule assembly were seen in the production of c-mitoses. Instead, anaphases were well represented and served to identify the presence of five more or less metacentric chromosomes (Figs. 1–2). Of the rest, two were telocentric and five markedly sub-metacentric or acrocentric. Spore mother cells with twelve bivalents at metaphase-I of meiosis confirmed this assessment (Fig. 4), but, even in material which had not been subjected to high temperatures, meiosis was remarkable for its irregularities. They included the production of bridges at anaphase-I (Figs. 5–9), as well as the subsequent exclusion of one or two fragments and/or univalent chromosomes from the daughter nuclei at telophase-I (Figs. 10–14).

At 10°C, pre-meiotic interphase nuclei included a considerably smaller block of heterochromatin (Fig. 15) than corresponding cells in mitotic interphase (Fig. 16). The only heterochromatin during leptotene occurred as two short but equal chromosome lengths which remained separate from each other, as they appeared to do throughout zygotene and pachytene into diplotene. Despite the fact that these two segments were not seen to synapse, it would appear that they did belong to homologues, one end of each being heterochromatic and the other euchromatic. Thus, they were seen during diplotene to be held in bivalent form by a chiasma in the euchromatic region (Figs. 17–20), this being the only identifiable bivalent and, hence, the only discovery of localized chiasmata within the complement. If anaphase irregularities were related to events at or before diplotene, they were not observed, nor was it possible to identify diakinesis as anything other than normal (Fig. 21). Abnormalities associated with metaphase-I were numerous, though by no means common, and concerned the presence of occasional univalents and/or fragments. Only from anaphase-I onwards, however, was there evidence of large scale irregularity.

Many cells underwent what appeared to be an undisturbed first anaphase complicated only by slight asynchrony between bivalents (Fig. 22). By far the greatest number of anaphases, however, involved some form of bridge. Relatively few were associated with fragments or univalents. Most were greatly extenuated but showed localized thickening at the center (Figs. 5–8), and it was in an attempt to identify the nature of this thickening that the specimen was then subjected to a raised temperature.

Temperatures of 20–25°C had two main effects on the first meiotic division (Fig. 23). They would appear to have affected zygotene and/or pachytene in reducing or preventing synapsis and/or chiasma formation, as a result of which the frequency of unpaired chromosomes at metaphase-I was greatly increased. Indeed, most cells of this sort included 24 univalents (Fig. 24). Such cells would then appear to have become susceptible, along with cells already in later stages of first meiosis, to the second type of influence exerted by increased temperature, which was restricted to cells at metaphase-I and anaphase-I. At both stages the effect was to arrest meiosis, and this was associated with chromosome de-spiralization. This was true whether the chromosomes were univalent or bivalent. Since it was found that de-spiralized chromosomes retained their normal



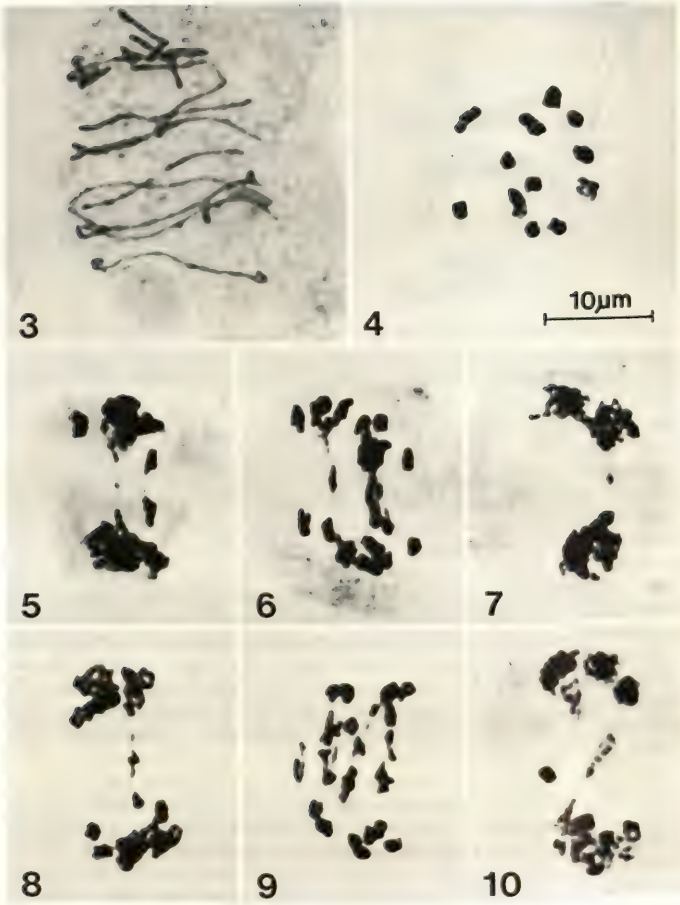
FIGURES 1–2. Gametophytic mitosis in *Hookeria lucens*, ×3025.—1. Onset of anaphase.—2. One pole at mid-anaphase.

positional relationship to each other (Figs. 25–27), it proved to be a phenomenon of immense value in elucidating the exact nature of anaphase bridges.

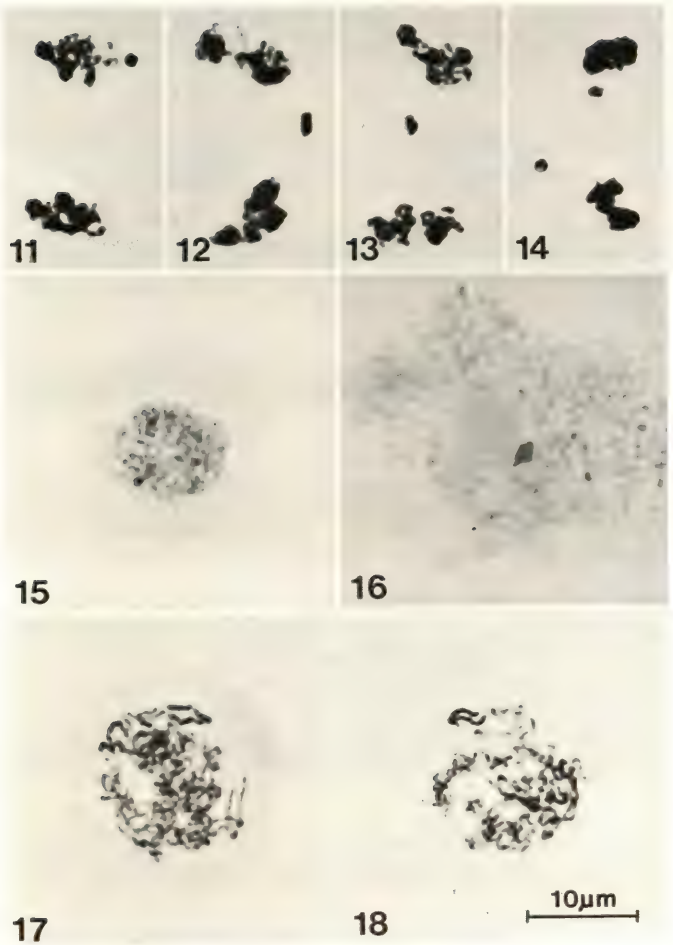
The majority of bridges were chromatid bridges bearing two parallel side-arms (Fig. 28). They were thus the outcome of sub-chromatid breakage and, depending on the position of chiasmata within the bivalent, of subsequent reunion or exchange between sister or non-sister half-chromatids (Fig. 29). It is noteworthy, however, that a large proportion of such bridges involved the only chromatid of each of the participating chromosomes (Figs. 30–31), for which two possible explanations exist. Either a pair of homologues had failed to replicate prior to synapsis, or the centromere of a univalent chromosome had divided synchronously with the onset of anaphase-I (Fig. 29c). The type of bridge illustrated in Figure 8 could clearly be interpreted in terms of lateral displacement of parallel side-arms (Fig. 29d), a phenomenon which would account for the generally rhomboidal shape of the central thickenings of anaphase-I bridges. Indeed, it might be suggested that only when the bridge is broken do the side-arms lie parallel to each other in the normally condensed state (Fig. 9).

Neither in the population as a whole nor within individual capsules of this specimen of *Hookeria lucens* was meiosis synchronous in different spore mother cells. It was therefore possible to observe that spontaneous meiotic irregularity at 10°C involved univalents at metaphase-I and bridges at anaphase-I and persisted throughout the second division. In general, two or three fragments or univalent chromosomes were excluded from the four restitution nuclei of telophase-II. At 20–25°C, however, meiosis was arrested and did not proceed to the second division. Irregular numbers of chromosomes became associated in intensely staining groups (Figs. 25–26) which could not be referred to as nuclei, albeit deficient nuclei, because nuclear membranes did not appear to develop. Their accumulation within a capsule tended towards a situation in which virtually every spore mother cell was thus affected.

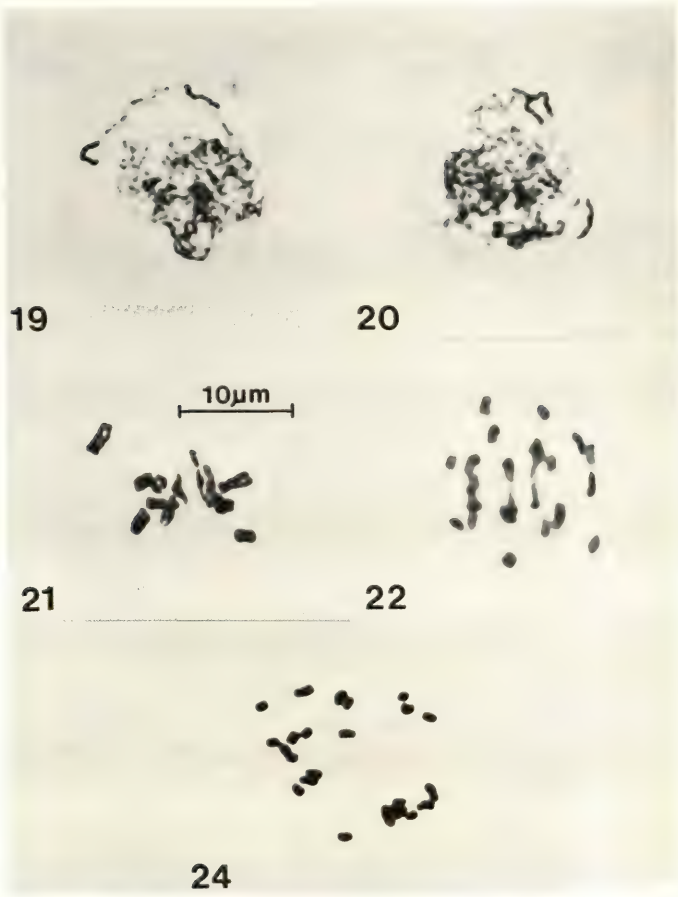
Subsequent assessment of the viability of spores in 25 mature and perfectly developed



FIGURES 3–10. Chromosome configurations in *Hookeria lucens*, ×2050.—3. Gametophytic late prophase showing nucleolar organizing chromosome below.—4. Metaphase-I of meiosis.—5–9. Anaphase-I of meiosis with bridges resulting from half-chromatid breakage and reunion.—10. Bridge and fragment/univalent at telophase-I of meiosis.



FIGURES 11–18. Chromosome configurations in *Hookeria lucens*. ×2050.—11–14. Telophase-I of meiosis with excluded fragments/univalents.—15. Pre-meiotic interphase showing extent of heterochromatin.—16. Mitotic interphase with nucleolar associated heterochromatin.—17–18. Diplotene with partially heterochromatic bivalent above.



FIGURES 19–22, 24. Meiotic chromosome configurations in *Hookeria lucens*. × 2050.—19–20. Diplotene with partially heterochromatic bivalent above.—21. Diakinesis.—22. Anaphase-I.—24. Twenty-four univalents at metaphase-I following heat shock.

capsules at dehiscence revealed a high proportion of capsules, amounting to 60% of the total, in which no viable spores were found. It is suggested that these were capsules in which meiosis was subjected to a raised temperature. There was also substantial abortion in the remainder. Only between 18% and 48% in any one capsule were fully turgid.

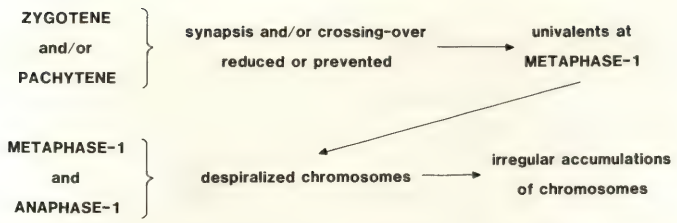
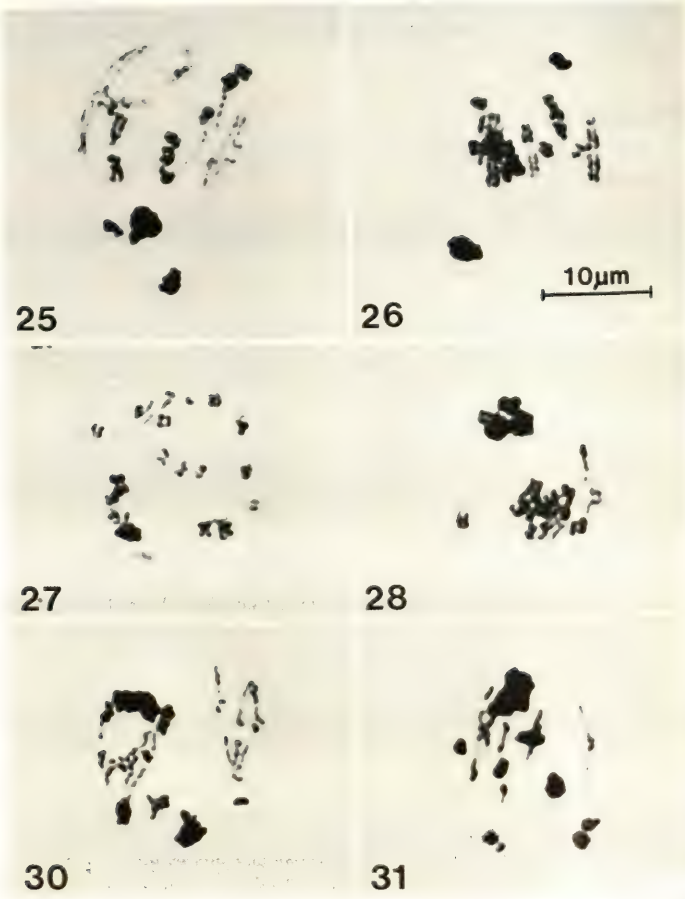


FIGURE 23. The effect of increased temperature on meiosis in *Hookeria lucens*.

containing chloroplasts. The size of these spores, as related to diameter, varied both within and between capsules, but an analysis of variance identified a significant difference between just one pair of capsules in this respect at the 5% level and no significance at the 1% level. On pooling the data, where N = 980, it was therefore found that mean spore size was 20·6955 ± 0·1535 μm with a 95% range of 15·8902–25·5008 μm. Variation about the mean was not that of a normal distribution (χ^2 = 93·8931, P <0·001), but by plotting it on a probability scale its nature could be deduced. The central straight line component in Fig. 32 could be regarded as indicative of a normal distribution, whereas the upper and lower deviations suggest the inclusion of abnormal spores amounting to about 5% in each tail. When expanded to cover the full range of probability, the central portion reaches the 50% level at a point which indicates a mean diameter of 19·825 μm, only slightly lower than the calculated value.

Discussion. Examples of meiotic irregularity in mosses are widespread in the literature, but until now none had been investigated thoroughly. Indeed, Anderson (1964) pointed out that meiosis is imperfectly understood in mosses and considered it to be related to the brevity of prophase-I compared with subsequent stages, and it is undoubtedly true that references to anything other than metaphase-, anaphase- and telophase-I and anaphase- and telophase-II are exceedingly rare. A notable exception is Dill's (1964) description of dictyotene, a stage of chromatin dispersion intercalated between diplotene and diakinesis in *Hypnum circinale* Hook., *Brachythecium frigidum* (C. Müll.) Besch., and *Claopodium crispifolium* (Hook.) Ren. & Card. Evidence that dictyotene occurs during meiosis in *Hookeria lucens* has not been found, nor was it described by Vaarama (1954) in *Pleurozium schreberi* (Brid.) Mitt. Dill (1964), however, reported that diplotene was unnaturally transitory at room, as opposed to field, temperature and therefore suggested that if diplotene were overlooked, dictyotene might then be mistaken for leptotene or zygotene. As a result, the conclusion might be drawn that all subsequent stages up to metaphase-I were of equally short duration. Such is not the case in *H. lucens*, however, since diplotene and diakinesis were observed repeatedly, thereby implying that dictyotene is not a universal feature of mosses.

At the temperatures likely to be encountered by this species in the field, meiosis was found to proceed to completion despite the presence of aberrations which resulted in bridge formation and irregular segregation. Since both phenomena result in deletion or duplication, it is perhaps in those terms that, in capsules containing some viable spores, the 10% of abnormally large and small spores (5% in each tail) should be interpreted. It



FIGURES 25–28, 30–31. Heat induced chromosome uncoiling during meiosis in *Hookeria lucens*. ×2050.—25. Detail of acrocentric bivalent (left) and telocentric bivalent (right), both with unterminalized chiasmata. Note irregular accumulation of densely staining chromatin.—26. Detail of telocentric bivalent with terminalized chiasma (right) and irregular accumulation of chromatin.—27. Detail of univalents.—28. Detail of bridge with parallel side-arms in bivalent to right.—30. Detail of broken bridge with parallel side-arms in univalent or unreplicated bivalent (second from right).—31. Detail of bridge with parallel side-arms in univalent or unreplicated bivalent (right).

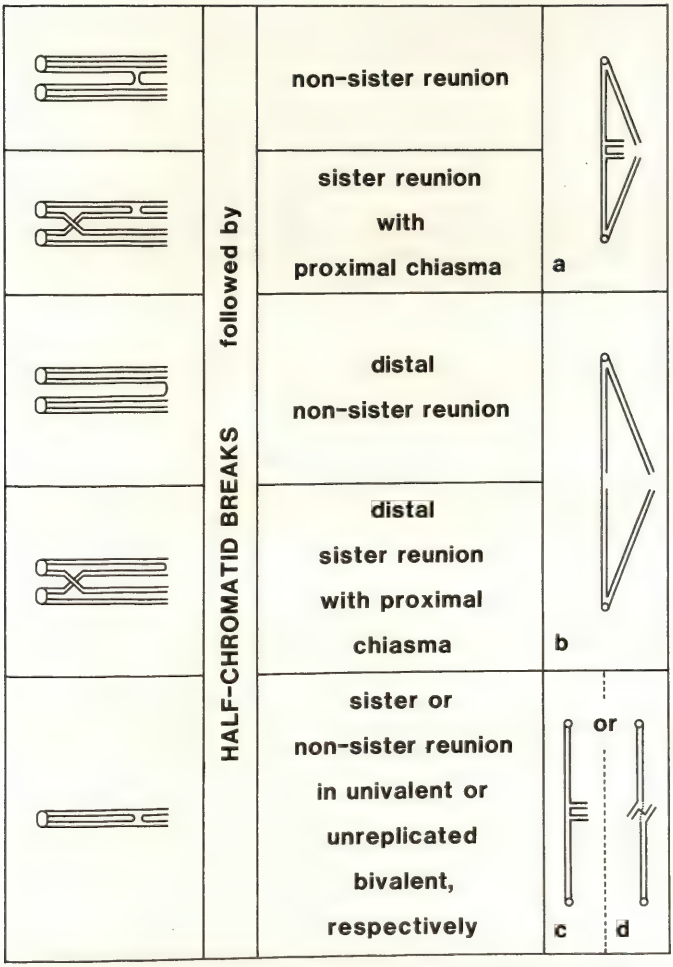


FIGURE 29. The consequences at anaphase-I (right) of the pachytene events illustrated (left).

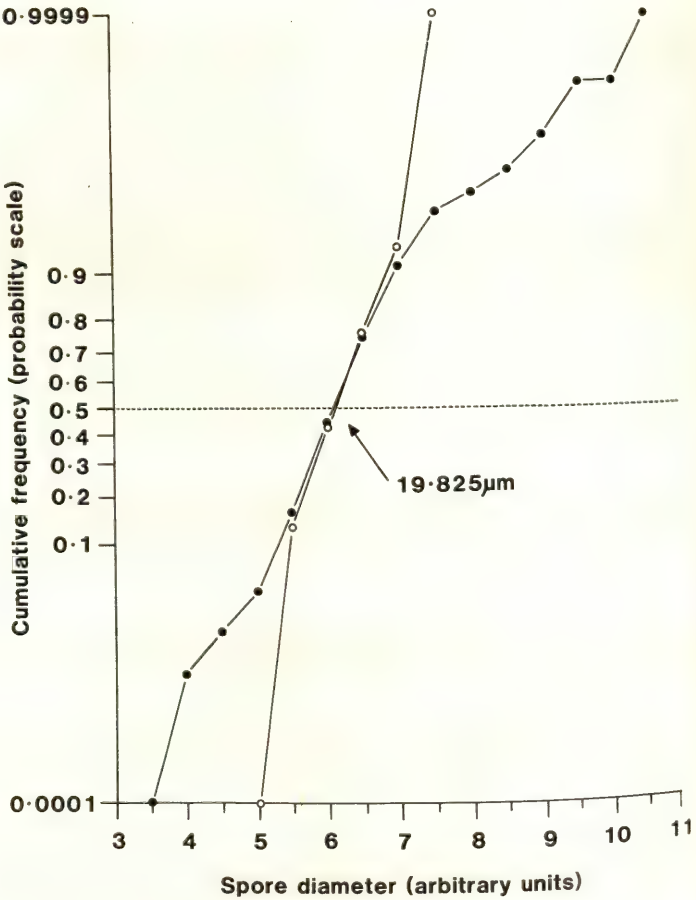


FIGURE 32. Size frequency among viable spores (●) compared with the normal component (o).

might be argued that their exceptional size is related to surviving chromosomal duplication and deficiency, respectively, more serious genetic imbalance being reflected in the 52%–82% abortion found in the same capsules. It should be emphasized, however, that evidence has been put forward to suggest that the size of apparently unaffected spores was considerably larger than taxonomic descriptions of this species acknowledge (e.g. Smith,

1978*a*; Nyholm, 1960). Smith (1978*a*), for example, defined a range of 12–16 μm in British material compared with a 95% range of about 16–25·5 μm among apparently normal spores of the present specimen. In European material as a whole, Nyholm (1960) reported 16–18 μm, whereas Limpricht (1895) and Engler and Prantl (1909) recorded 10–16 μm.

As the first detailed analysis of anaphase-I bridges in a moss, this report suggests the need for a careful reappraisal of similar meiotic irregularities in other monoecious species where their presence has been widely interpreted as an indication of outbreeding (e.g. Ramsay, 1973; Richards, 1978; Smith, 1978*b*). The underlying cause of half-chromatid breakage and subsequent reunion and/or interchange in *Hookeria lucens* is unknown, but there is no reason to suppose that it must stem from hybridity, although Thompson and Woodruff (1978) implicated outbreeding in the phenomenon of chromosome breakage and male recombination in *Drosophila melanogaster* Meig. Bennett (1977) described late replicating telomeric DNA as a cause of mitotic bridge formation in *Triticale* endosperm. Any effect this might have on meiosis, however, would be expected during the second anaphase as well as the first. Alternatively, chromosome breakage may be genetically determined, as it is for example in the mosquito *Aëdes aegypti* (L.) (Newton, Wood & Southern, 1976) and in inbred rye (Rees & Thompson, 1955), but errors of crossing over at pachytene are another possibility. Both this and its possible origin in lesions arising during pre-meiotic DNA replication are compatible with the view of Kaina (1979) that aberrations are more frequent in euchromatin than heterochromatin. Thus, if the heterochromatic bivalent of *H. lucens* had been involved in bridge formation, it could not have been via the heterochromatic segments, since they were invariably seen to be held together during diplotene only by a chiasma in the adjacent euchromatic region.

Lewis and John (1966) considered that exactly similar bridges to the ones found in *Hookeria lucens* are common in higher plants and animals. That this should be so was correlated with their opinion that errors in the process of crossing over could be expected to be frequent. These authors also claimed that many reports of inversion hybridity based on the observation of anaphase-I bridges would, on re-examination, prove to have been incorrect. In view of the present work with *H. lucens*, it would be of interest to investigate the possibility in the wider context of other bryophytes, particularly as univalent or unreplicated bivalent bridges have so far been seen only in this one moss. Indeed, indications that anaphase bridges with parallel side-arms resulting from half-chromatid breakage may not be unique to *H. lucens* among mosses do already exist in the literature. Steere, Anderson, and Bryan (1954), for example, illustrated a similar type of bridge in *Orthotrichum rupestre* Schleich. ex Schwaegr., as did Newton (in Smith, 1978*b*) in *Brachythecium rutabulum* (Hedw.) B.S.G.

The induction of further meiotic irregularities by increasing ambient temperature undoubtedly proved helpful in determining the nature of spontaneous aberration in *Hookeria lucens*. At least as important, however, are the far-reaching implications it has for bryophyte cytology in general, and it is vital that their magnitude should be thoroughly understood. It is common practice for cytologists to allow immature capsules, collected in the field, to develop in the laboratory to the stage at which meiosis occurs. Temperatures of 20–25°C can well be expected from time to time in many laboratories, making it pertinent to consider their affect on the material. Ramsay and Schofield (1981) recognized the possibility that some at least of the meiotic irregularity noted in mosses may be attributable to environmental conditions, but the observation carries much deeper

implications, too. As Smith (1978*b*) has observed, complete asynapsis or desynapsis has been rarely reported. Smith and Newton (1968) reported it in *Brachythecium velutinum* (Hedw.) B.S.G., and a significant degree has been found in *Grimmia* cf. *asperitricha* Dix. & Sainsb. (Newton, 1980), but there are accounts in the literature which suggest that the same phenomemon may have been misinterpreted elsewhere. For instance, a permanent slide of meiosis in a specimen of *H. lucens* in which multivalent formation was tentatively identified (Smith & Newton, 1968) clearly shows the irregular accumulation of univalents reported in the present paper. Conversely, *Philonotis turneriana* (Schwaegr.) Mitt. with $n = 12$ (Verma & Kumar, 1980) seems to owe its description to unrecognized asynapsis or desynapsis in a specimen with $n = 6$, and it is probable that other examples also exist. Thus, the specimen of *Camptochaete ramulosa* (Mitt.) Jaeg. in which Ramsay (1974) reported $n = 22$ displayed all the characteristics associated with univalent meiosis in *H. lucens*. Many authors (e.g. Steere, 1972; Smith, 1978*b*) have drawn attention to the possibility of putative cases of aneuploidy being attributable to different interpretations of the same karyotype. The present work emphasizes the need for extreme caution in all meiotic analyses in mosses. Since nothing is known about the optimum temperature at which meiosis proceeds undisturbed, there is good reason to supply as much detail as possible about the conditions to which pre-meiotic capsules are known to have been subjected prior to examination. Anderson and Crum (1958) reported normal meiosis as low as 0–5°C in many species, and it has now been found to involve asynapsis or desynapsis at 20–25°C in *H. lucens*. Knowledge of the generality of these observations and of behavior in the intermediate range is thus of immense consequence and deserves detailed study.

Two further points of interest emerge from this work, and both relate to mitosis. The first concerns the practical detail that prolonged treatment of up to 6 hours with colchicine or 8-hydroxyquinoline failed to arrest mitosis, thereby suggesting that with cell cycles of 48–90 hours (Hallet, 1976), this species and perhaps others will require even more prolonged immersion in such solutions. The second point relates to chromatin expression in the gametophytic interphase compared with pre-meiotic interphase, there being less heterochromatin in the latter. It raises the interesting possibility that at least some of the gametophytic heterochromatin is facultative, a type already known among bryophytes in *Plagiochila praemorsa* Steph. (Berrie, 1974) and *Dicranum tauricum* Sapehin (Newton, 1977). Moreover, it should be borne in mind in this context that Inoue and Himeno (1978) described 2H- and 2h-chromosomes in the gametophytic complement of *Hookeria lucens*, whereas significant amounts of heterochromatin have been seen during the present study in only one pair of meiotic homologues.

It is a pleasure to offer this paper in honour of the seventieth birthday of Lewis E. Anderson, whose work continues at the forefront of bryophyte cytology.

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CYTOLOGICAL AND SEXUAL CHARACTERISTICS OF THE MOSS *DICRANOLOMA* REN.[1]

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Abstract. In *Dicranoloma*, a primarily Southern Hemisphere (76 of 112 species) genus closely related to the Northern Hemisphere genus *Dicranum*, there are 22 species listed for Australia, but little is known about more than a few of these. The genus is usually sexually dimorphic with dwarf males epiphytic on female plants. Chromosome numbers have been reported for a few species (Ramsay 1967, 1974), but a detailed analysis of cytology and sexuality in *Dicranoloma* has not been explored previously. Cytological details for 5 species, *D. dicarpum*, *D. robustum* var. *setosum*, both with $n = 7$; *D. menziesii*, $n = 8(7+m)$; *D. serratum*, $n = 9(7+2m)$; and *D. billardieri*, $n = 12, 13$ are described. The development and distribution of male and female plants from both field collections and culture experiments is discussed. Possible bases for sex determination in the genus are outlined, and similarities between *Dicranum* and *Dicranoloma* discussed.

The genus *Dicranoloma* Ren., while closely related to the Northern Hemisphere *Dicranum*, is distributed mainly in the Southern Hemisphere. Taxonomic differences used to separate the two genera include structure and shape of basal leaf cells, presence of a hyaline leaf border, thin costa, and robustness of plants, but the size and structure of the peristome teeth is the most reliable character (Sainsbury 1955, Takaki 1966, Noguchi 1959, Scott & Stone 1976). *Dicranum* and *Dicranoloma* occupy similar ecological niches, occurring in damp forests and forming extensive patches on trunks, roots and rotting logs.

As a genus, *Dicranoloma* is represented in the moss floras of South America, South Africa, Australasia, and Oceania, with a northwards extension into southeastern Asia and Japan Wijk et al. (1962). Within Australia the genus occurs almost exclusively in the eastern states (Fig. 48) with a total of 19 endemic species, or 86% of the Australian representatives. There are six species which occur in both Australia and New Zealand, while two of these species extend more widely: *D. menziesii* (New Zealand, South America, and Oceania) and *D. billardieri* (South America, Africa, New Zealand).

The only records of chromosome numbers in *Dicranoloma* are five species from Australia (Ramsay 1967, 1974): $n = 7$ [*D. dicarpum* (Nees) Par., *D. robustum* (Hook.f. & Wils.) Par. var. *setosum* (Hook.f. & Wils.) Sainsb.]; $n = 8(7+m)$ [*D menziesii* (Hook.f. & Wils.) Par.]; $n = 9$ (7 + 2m) [*D. serratum* (Broth.) Par.]; $n = 12, 13$ [*D. billardieri* (Brid.) Par.]. Cytological details and behavior at meiosis were not discussed in detail in Ramsay (1974). In the related genus *Dicranum* a range of chromosome numbers has been recorded, $n = 8, 9, 10, 12, 13, 14, 24$ (summary in Fritsch, 1982; see in particular, Briggs, 1965; Ramsay, 1969; Smith & Newton, 1968; Crum & Anderson,

[1]Some of the information in this paper under this title was presented at ICSEB II Vancouver, 1980. *Acknowledgments*: The writer is deeply indebted to Miss Meera Jayachandran for technical help in preparing and maintaining cultures as well as for some of the data collection such as frequency of dwarf males in *Dicranoloma*. A. Murray kindly collected some of the specimens used. The research received support from the Australian Research Grants Scheme to whom the author is indebted.

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1981; Lazarenko et al. 1971), with much intraspecific aneuploidy. The chromosome number $n = 7$ and the large chromosomes found in *Dicranoloma* have also been reported for *Orthodicranum montanum* (Visotskaya, 1975), *Kaieria falcata, K. starkei* [as *Arctoa* (Visotskaya, 1972), from Europe; Visotskaya, 1967, Lazarenko et al., 1971], and *Dicranum muehlenbeckii* (Visotskaya, 1975). Other species in these genera are of primary polyploid origin, e.g. $n = 14 (13 + m)$, *Kiaeria blytii* (Ireland, 1965), while *K. starkei* has $n = 7$ and $n = 14$ cytotypes in U.S.S.R. (Lazarenko et al., 1971, Visotskaya, 1972) and $n = 14 (13 + m)$ in U.S.A. (Ireland, 1965) and Canada (Ramsay, 1983). In *Dicranum* and *Orthodicranum* variable numbers have been reported (Fritsch, 1982), e.g. Smith and Newton (1968) record $n = 8$ for *O. scottianum* in Great Britain. The number $n = 12$ occurs more frequently than any other in these two genera, being found in all four species of *Orthodicranum* for which records are available and in twelve of the seventeen species of *Dicranum*.

The family Dicranaceae contains the largest number of genera (10) among mosses with pronounced sexual dimorphy (Ramsay, 1979). While Brotherus (1924) records *Dicranoloma* as characteristically having "zwergmächen," in type descriptions for many of the species and in subsequent studies, details of sexuality are not given and in some have never been determined where sporophytes have not been located. No experimental culture or field techniques for studying sexuality in *Dicranoloma* have been reported, although investigations on *Dicranum* both published (Briggs, 1965) and unpublished (Loveland, 1956) provide some interesting data.

Previous work to ascertain the nature of sex determination in mosses on *Dicranum* (Loveland, 1956; Briggs, 1965), *Homalothecium* (Wallace, 1970), and *Macromitrium* (Ramsay, 1966*a, b*, 1979; Ramsay & Berrie, 1982; Une, 1983; Ramsay & Vitt, 1983) has failed to resolve the question of whether the apparent sex chromosomes control sexuality or whether dwarfness of males is genetically or physiologically determined in these genera. Evidence seems to favor genetic control in some (*Macromitrium, Dicranum*) and physiological control (*Homalothecium*) in others. Ramsay and Berrie (1982) discuss some preliminary investigations on the genera *Macromitrium* and *Dicranoloma* in relation to sex determination. Table 1 in their publication summarized the chromosome numbers and sexuality in *Dicranum* and *Dicranoloma*. In the present study a more detailed account of the cytology and sexuality of *Dicranoloma* in Australia is presented. The results must however, still be considered preliminary.

Materials and Methods

MATERIALS. The specimens used in these studies included living material collected by the author for cytological, spore germination, and development stages, while herbarium specimens were examined for sexuality and characteristics of dwarf males. Details of the total list of materials examined is found in Appendix 1. Voucher specimens for all Ramsay collections listed are located either in SYD (some chromosome vouchers) or UNSW.

METHODS. *Cytological*: Specimens were studied immediately after collection or kept in polyethylene bags in the laboratory or cool room at 15–20°C until capsules matured. Meiosis was studied using aceto-orcein or aceto-carmine squashes and slides made permanent using dry ice as previously described (Ramsay 1966*b*, 1969, 1974).

METHODS. *Germination and Development*: Culture and growth studies were carried out using Bold's basal medium or White's culture medium in 2% agar and grown in a cabinet

supplying a lighting regime of 16 hours light at 2000 LUX. Germination stages were recorded, as well as time for production of dwarf males, morphology of male plants etc. Some cultures were maintained for up to 18 months at time of writing.

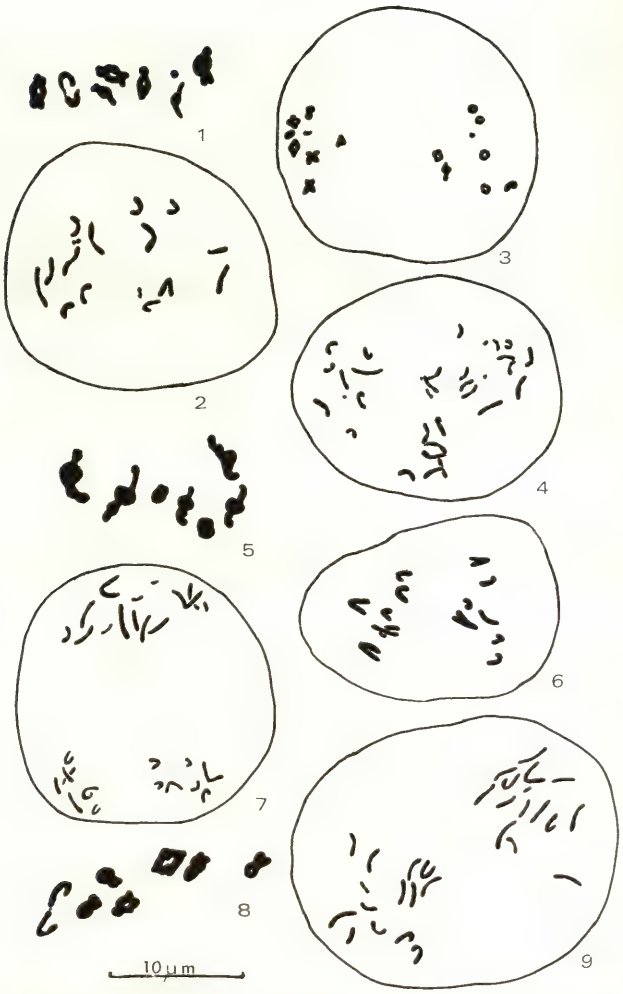
METHODS. *Dwarf males*: Sexuality of specimens was determined and the morphology of males and females recorded from herbarium as well as living material. Dwarf males from living specimens were cultured: (a) excised from female and planted directly onto agar; (b) excised from female and grown on medium containing crushed female extract. Regeneration from female leaves and stem fragments on nutrient agar was attempted.

METHODS. *Other studies*. The distribution of dwarf males in collections (both living and herbarium) of moss specimens was determined. Each upright shoot in a collection was searched and the location as well as numbers of dwarf males present recorded. The number of sporophytes was noted and the sex of each shoot determined where possible, if no sporophyte was attached.

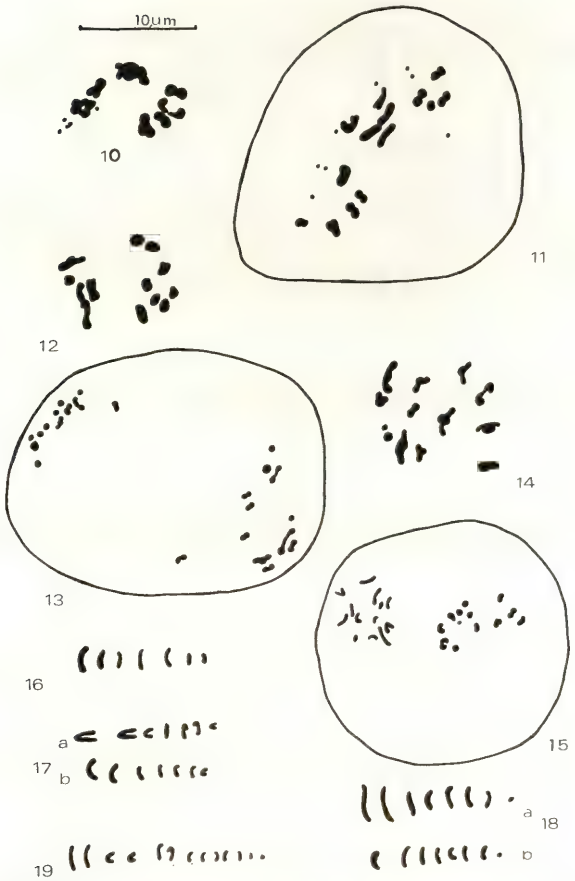
Taxonomy. Taxonomic revision of *Dicranoloma* have been published for Japan (Takaki, 1966), New Zealand (Sainsbury, 1955) and Southern Australia (Scott & Stone, 1976; Catcheside, 1980), but no revision of Australian species as a whole has been undertaken. Scott and Stone (1976) consider that *Dicranoloma robustum* and *D. billardieri* are synonymous, as the polymorphism of these species makes it difficult to delineate them. However, they do confess that "there may be several species involved in the complex group but the task of sorting out the mixture is a formidable one and not to be undertaken in the herbarium alone nor in Australia in isolation from the rest of its distribution." At present from my own observations and until such a revision is carried out, I prefer to maintain them as separate species since they may be found growing together but recognisably different. Scott and Stone (1976) also suggest that *Dicranoloma trichopodum* should be retained as a *Dicranum* although the hyaline border characteristic of *Dicranoloma* is present, while several other species named as *Dicranum* need careful re-examination.

Cytology. The bivalents of *Dicranoloma* are characteristically large in the 7, 8, and 9 chromosomes species, *D. dicarpum, D. menziesii, D. robustum* var. *setosum, D. serratum*, (Figs. 1,5,8), and small in *D. billardieri*, which has $n = 12$ or 13 chromosomes (Figs. 12,14). Diakinesis stages are well developed and bivalent shape variable with mostly interstitial chiasmata, only one or two smaller bivalents having terminal chiasmata by metaphase I. In most species one bivalent divided precociously and in some cells appeared slightly dimorphic (*D. robustum* var. *setosum, D. menziesii, D. dicarpum, D. serratum*). It was not necessarily the largest in the complement.

Anaphase stages (both AI and AII) are particularly clear in *Dicranoloma*, and the morphology of the somatic-like chromosomes could be determined well enough to examine the karyotypes of several species, *D. dicarpum, D. menziesii*, and *D. billardieri* (Figs. 20–22). Form percent and relative length of chromosomes have been estimated (Table 1) showing the presence of microchromosomes in two species, *D. menziesii* and *D. serratum* (Ramsay, 1974), and their behavior in *D. serratum* (Figs. 33–36) was found to be comparable with reported behavior in *Dicranum majus* (Vaarama, 1950, 1968). The m-chromosomes disjoined precociously and, in some, chromatid division preceded first anaphase (Figs. 11, 33, 34, 36). The chromosome number $n = 12$, 13 ($12 + m$) in *D. billardieri* was obviously derived by polyploidy with subsequent loss of chromosome material (Fig. 22). This reduction in number may be by translocation from a fourteenth chromosome to others in the complement or erosion of or almost complete loss of genetic



FIGURES 1–9.—1–4. *Dicranoloma menziesii*—1. M-I, note minute bivalent.—2. A-I, somatic-like chromosomes.—3. M-II.—4. A-II.—5–7. *D. dicarpum*.—5. M-I.—6. A-I.—7. A-II.—8–9. *D. robustum* var. *setosum*.—8. M-I, one bivalent disjoining early.—9. A-II.



FIGURES 10–19.—10–11. *D. serratum*.—10. M-I, two minute bivalents already disjoined, one of the half bivalents separating into chromatids.—11. A-I, m-chromosomes already divided into chromatids.—12–15. *D. billardieri*—12–13.—(n = 12).—12. M-I.—13. M-II.—14–16. (n = 13).—14. M-I, two minute bivalents.—15. A-I.—16. *D. robustum* var. *setosum*, alignment of A-II chromosomes (from Fig. 9).—17. *D. dicarpum*, alignment of A-I (from Fig. 6), and A-II (from Fig. 7) chromosomes.—18. *D. menziesii*, alignment of A-I (from Fig. 2) and A-II (from Fig. 4) chromosomes.—19. *D. billardieri* (n = 13) alignment of A-I chromosomes (from Fig. 15).

TABLE 1. Chromosome size in *Dicranoloma*.[a]

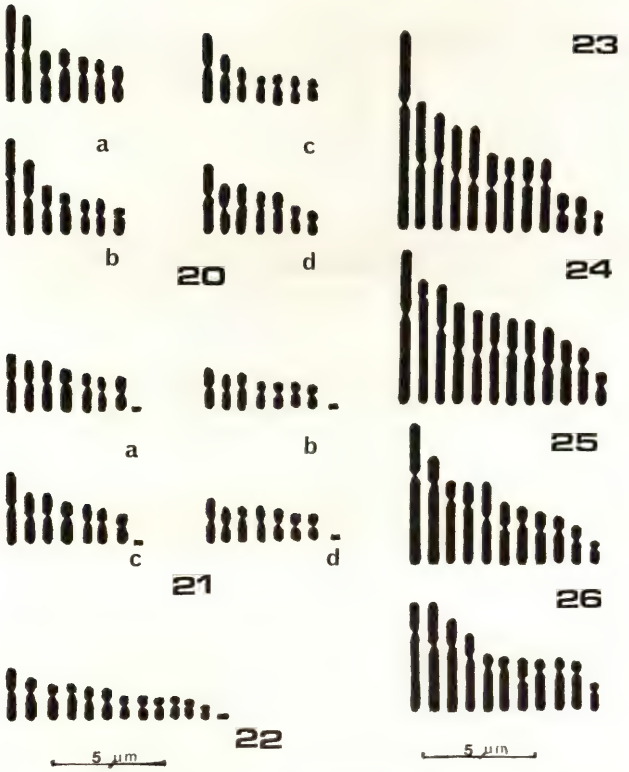
Species	Relative lengths of chromosome												
	Chromosome number												
	1	2	3	4	5	6	7	8	9	10	11	12	13
D. dicarpum	21.7	21.7	13.1	13.1	10.9	10.9	8.7						
D. menziesii	16.4	16.4	16.4	13.7	13.7	11.0	11.0	0.14					
D. billardieri	14.3	12.0	9.5	9.5	9.5	9.5	7.1	7.1	5.9	5.9	4.7	3.6	1.1
Species	Form %												
	Chromosome number												
	1	2	3	4	5	6	7	8	9	10	11	12	13
D. dicarpum	50	40	40	50	40	50	50						
D. menziesii	42	50	50	40	40	50	50	—					
D. billardieri	50	40	33	33	50	50	50	50	40	40	50	50	—

[a]As studies are based on meiotic chromosomes actual length is not included but Form % $\left(\text{i.e. } \frac{\text{short arm}}{\text{total chrom. length}}\right)$ and Relative Length (length as % total length all chromosomes) are used for comparisons.

material from one chromosome to give $n = 13$ or two to give $n = 12$. All chromosomes except the smallest three and the two large ones fall naturally into pairs, reflecting their polyploid origin. The two largest chromosomes in *D. dicarpum* (Fig. 20) exceeded the next in size, whereas this difference was not present in *D. menziesii* (Fig. 21). In all species examined apparently heteromorphic bivalents were observed (Fig. 27–31). These were not necessarily the largest. The early disjunction of this bivalent and the somatic appearance of its homologues was characteristic. A similar bivalent has been reported in *Dicranum* (Briggs, 1965; Anderson, 1980). Anderson has designated it a sex bivalent in *D. spurium*, while Crum and Anderson (1981) also report an X/Y sex bivalent in "*D. condensatum*."

The smaller chromosomes of *Dicranoloma billardieri* were similar in size to those of *Kiaeria starkei* ($n = 14$) and *D. scoparium* ($n = 14$) from Canada (Ramsay, 1983). Although there are seven chromosome cytotypes in *Kiaeria, Orthodicranum* and *Dicranum* (refer to Fritsch, 1982) the bivalents are not so large as those in *Dicranoloma*, nor do they appear (from illustrations) to have the distinct diakinesis stages and bivalent shapes. However, drawings chosen to represent the chromosome numbers in most publications do not attempt to show the variety of morphologies seen in a particular species.

The possibility that the heteromorphic bivalent may represent sex chromosomes needs studies of male and female karyotypes, and this has not been done nor is it possible where dwarf males are present (Ramsay & Berrie, 1982). Comparison of chromosome pairs in sporophytic mitoses might assist. The AI and AII karyotypes as displayed in Figures 20–22 show some variations in the homologues in *Dicranoloma billardieri* (Fig. 20a, b) in chromosome 2 but in the AII group differences are present in a number of chromosomes. The AI and AII chromosomes of *D. menziesii* (Fig. 21) show much more uniformity. As the chromosomes are extremly small at these stages it is difficult to know how reliable the differences are. The dimorphism of the bivalent in species studied is not pronounced and would be difficult to recognize in larger chromosomes. All species



FIGURES 20–26. Estimated kartyotypes of *Dicranoloma* and *Dicranum*. Note variation between species and presence of large chromosomes in each. Sub-telocentric chromosomes present in chromosome 2 of *D. bonjeani*. Some chromosomes in each fall naturally into pairs by length but variation in centromere position is sometimes present. The chromosomes of *Dicranum* and *Dicranoloma* are drawn to the same scale but differences in chromosome size may be due to the stages of division and not to the actual size differences between the genera.—20–22. *Dicranoloma* species based on meiotic studies.—20 a,b,c,d. *D. dicarpum* n = 7. a,b AI chromosomes. c,d. equivalent AII chromosomes.—21 a,b,c,d. *D. menziesii* $n = 8(7+m)$ note extremely small size of m-chromosome. a,b. AI chromosome. c,d. equivalent AII chromosomes.—22. *D. billardieri* $n = 13$; note smallest chromosome is an m-chromosome. One AI chromosome complement.—23–26. *Dicranum* species (from Great Britain) based on mitotic studies of female complements.—23. *D. scottianum (Orthodicranum).*—24. *D. bonjeani*.—25. *D. majus*.—26. *D. scoparium*.

TABLE 2. Summary Dwarf male characteristics of some *Dicranoloma* species.

	Size ♀ Plants (cm)	♀ Leaf size (mm)	Size Dwarf male plant (mm)
Dicranoloma menziesii	2–5	5–13	0.5–0.8
Dicranoloma robustum	3–12	5–15	0.2–0.5
Dicranoloma billardieri	3–10	5–8	0.5–1.0
Dicranoloma serratum	2–4	4	0.75
Dicranoloma dicarpum	2–5	8–9	0.3–0.8

studied were phyllodioicous including the derived primary polylpoid *D. billardieri*. It would be expected that doubling of chromosome number in a dioicous species would lead to monoicism. Ramsay and Berrie (1982) have proposed a scheme whereby reduction in chromosome number in polyploids that remain dioicous (assuming a sex chromosome mechanism is present) might be by loss of sex chromosomes. Another suggestion might be the maintenance of the duplicated sex chromosome by translocation onto its homologue so that genetic material would not be lost and pairing relationships would be defined. This would result in one or two large chromosomes. Such large chromosomes are present in both *Dicranoloma* and *Dicranum*, being more pronounced in *Dicranum*. A mechanism like this might explain the preponderance of the number $n = 12$ in *Dicranum* in which the base number is $x = 7$. In British species of *Dicranum* studied by Ramsay (1969, 1982*b*) one large chromosome was present (Figs. 24–26).

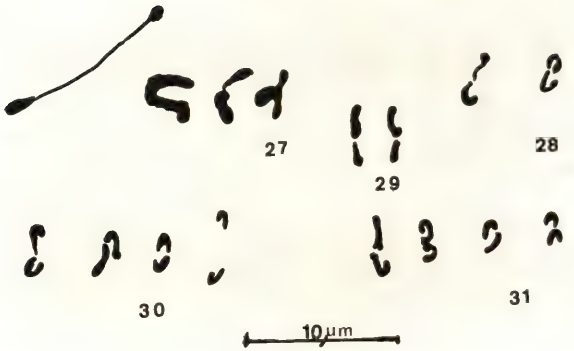
Further cytological studies on *Dicranoloma* in Australia will be published at a later date.

Characteristics of dwarf male plants. In *Dicranoloma* the dwarf male plants vary in size (Table 2) and degree of branching (Figs. 37–44), yet they are generally very similar in growth form between species or even intergenerically (see Ramsay, 1979; Ramsay & Berrie, 1982). When grown in culture, the earliest development is a bud bearing 3–8 leaves surrounding a perigonium containing 5–8 antheridia. A comparison between culture grown and naturally occurring dwarf males in *Dicranoloma* shows direct comparability in morphology (Ramsay & Berrie, 1982).

Dwarf males are found in *Dicranoloma* growing in the tomentum of the female branches well below the archegonia and occasionally on leaves. In a wide search of hundreds of shoots, males were not found just below the archegonia as recorded in the literature for some species (see Fleischer, 1920). The distance between the nearest males and archegonia was estimated as at least 1 cm. Their distribution is erratic within a population and on individual plants. When found, large numbers may occur together, *e.g.* 27 in *D. dicarpum* (Ramsay & Berrie, 1982). This sporadic occurrence is readily explained as due to spores falling irregularly or germinating in batches together and indicates quite clearly that they are not simple buds from the female plant. A persistent protonema seems to be present as reported by Briggs (1965) for *Dicranum*.

Tall and dwarf males were found in isolated populations of *Dicranoloma menziesii* and *D. dicarpum*. A comparison of female and the two types of male plants present in the population of *D. menziesii* studied shows distinct morphological differences even between large males (Figs. 45–47). Dwarf males occurred mostly on the stem surface attached to protonema but occasionally on leaves (Fig. 47).

No direct relationship between capsule production and presence or absence of dwarf males seems to exist. In female stems examined, some had up to 25 dwarf males but no



FIGURES 27–31. Heteromorphic bivalents in *Dicranoloma*. All exhibit premature disjunction.—27. *D. dicarpum*.—28. *D. menziesii*.—29. *D. robustum*.—30. *D. serratum*.—31. *D. billardieri*.

capsules while many with 1, 2 or more capsules had no dwarf males on the stem. Sperm must therefore transfer between stems in the moist tomentum to ensure fertilization. Minimum distance needed to be travelled by sperm could vary from several millimetres to several centimetres even on the same plant, while distance between plants would be greater.

In studies of *Dicranum majus* and *D. scoparium* in North Wales, Hughes (1980) noted that dwarf males were not found in association with barren female plants. He suggested that supply of antherozoids determined the extent to which polysety occurred in this genus and that the low frequency of fertilization observed in the field necessitated a mechanism to limit the number of archegonia produced. He made no study of the frequency of male plants in his work.

Observations from culture experiments. Preliminary investigations on two species, *Dicranoloma menziesii* and *D. dicarpum*, produced the following results.

(1) Dwarf male plants develop first in culture some maturing within 3–8 months.

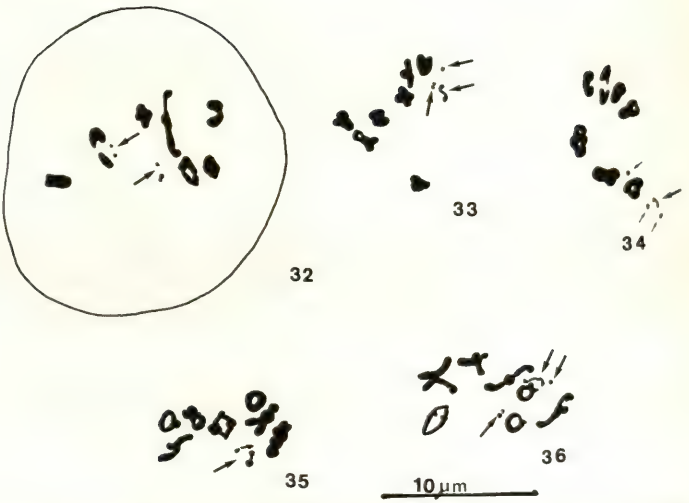
(2) The dwarf male protonema is persistent in culture, and (a) a new crop of dwarf males may be produced at intervals for at least a year or (b) a new crop of perigonia and antheridia may be produced on existing plants which are slightly larger than the first males.

(3) Protonema of two different kinds seem to be formed (until single spore cultures can be grown to maturity for females this is an observation rather than a statement of fact).

(4) There are morphological differences between male and female plants (Figs. 45–47), particularly in leaf structure (shape, degree development of costa and apex) but not cell shape and size (See Ramsay & Berrie, 1982).

(5) Distinct female plants, morphologically similar to adult females, appear about one year later and take much longer to mature (no archegonia in two years). Male and female plants can grow together when protonema are intermixed.

(6) The protonema does not spread along the surface of the medium but remains



FIGURES 32–36. Metaphase I meiosis in *Dicranoloma serratum*. Various MI plates to show behavior of m-chromosomes.—32. Two m-chromosomes separated into half bivalents (arrows). Hetermorphic bivalent present.—33, 34, 36. One m-bivalent separating, the other already disjoined with one half bivalent dividing (34) or divided (33, 36) into chromatids (arrow).—35. Two m-bivalents disjoining (arrows).

clumped, therefore gametophores are produced in close proximity to each other, and to the site of spore germination, possibly an adaptation to epiphytic lifestyle (see also *Macromitrium*, Ramsay, 1979).

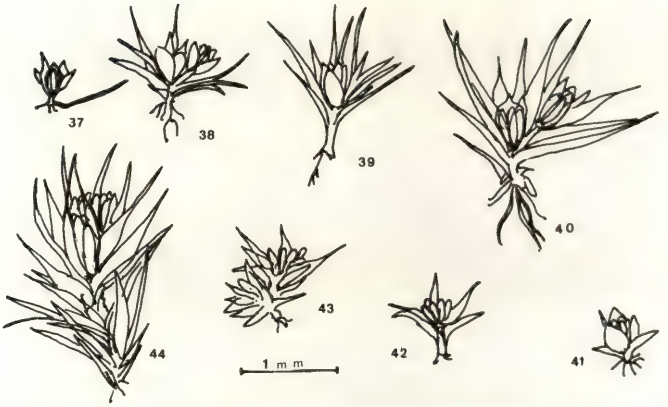
(7) Where large males are produced these bear very many perigonia (Fig. 46) or enlarged perigonia with large numbers of antheridia.

(8) Protonema may go through a period of arrested growth, and new growth develops the following year (evidence from old cultures which have not been subcultured for 6–10 months but are developing new protonema).

(9) The fruiting season for *Dicranoloma* extends over a large part of the year and plants can be collected in cytological condition at various times. This perhaps explains the function of a persistent male protonema.

Discussion

The nature and basis for sexual dimorphism has aroused much speculation since the discovery of reduced male plants by Schwaegrichen (1824) and later examples were illustrated and examined by Philibert (1883), Schellenberg (1920), Fleischer (1920) Nyholm (1954), and others. The experimental work of Ernst-Schwarzenback (1938, 1939, 1942, 1943) related sexual dimorphism to anisospory (called heterospory). Many more examples have been reported by Koponen (1971), Ando (1977, 1979), Ando and Fumamoto (1975), Peterson (1979). See Ramsay (1979) for summary. More recent studies



FIGURES 37–44. Dwarf males of *Dicranoloma dicarpum*. Note similarities in morphology and types of plants produced.—37–40. From field collections.—41–44. From cultures 8 months old.

on *Macromitrium* (Ramsay 1966*a*, 1979, 1982*a*, Ramsay & Berrie, 1982; Ramsay & Vitt, 1983; Une, 1983) and other mosses (Anderson, 1980) have indicated a possible relationship between chromosome dimorphism and dioicism, but Smith (1978) and Anderson (1980) still have reservations about whether the sex determining role has been demonstrated.

Briggs (1965) and Loveland (1956) carried out experimental studies related to cytological, taxonomic (Briggs), and sexual characteristics (Briggs and Loveland) of a number of *Dicranum* species. Within the four recognised taxa in Great Britain, Briggs found a great deal of cytological variation both in chromosome numbers and in the numbers of m-chromosomes present. All four species had some populations with such chromosomes, large heteromorphic bivalents occurred in *D. bonjeanii, D. majus* and *D. scoparium* while precocious separation of this bivalent was common.

Loveland (1956) examined *Dicranum* species in an effort to determine whether the basis of sex determination was genetical or physiological. He showed that the male plants were characteristic for each species with separable characters enabling each to be keyed out and that the cells in male plants were identical to those in female plants but reduced in number. The need for caution suggested by Ramsay (1979) in assuming that dwarf males on a species belong to that species has been borne out by recent studies on *Macromitrium* (Vitt pers. comm.), where a number of examples of dwarf males with papillose cells were detected growing on species with smooth cells. Care should therefore be taken in identifying males with the corresponding females.

Spore germination and regeneration experiments of both Briggs (1965) and Loveland (1956) gave interesting results. Briggs showed that dwarfness was genetically determined if dwarf males were always formed, *e.g. Dicranum majus*, but in others males were variable in size, *e.g. D. bonjeanii*, while in *D. scoparium* large and dwarf males both

FIGURES 45–47. *Dicranoloma menziesii*.—45. Female plant with sporophytes.—46. Large male, note many perigonia.—47. Dwarf male on leaf.

occurred and dwarf plants grew tall in culture. *Dicranum fuscescens* had only large males, which remained tall in cultivation. Field observations and herbarium studies seemed to suggest that the distribution of fruiting in these species is dependent on tolerance of dwarf males. They do not occur in the driest areas of Britain and were more drought-sensitive than female plants. The most sensitive to drought were dwarf male plants of *D. scoparium* found only in more oceanic parts of Britain. Thus variability in male plant size in species such as *D. scoparium* and *D. bonjeanii* and an indication of ecological selection for male size based on drought sensitivity suggest a genetical rather than environmental basis for sexual dimorphism (Briggs, 1965).

FIGURE 48. Distribution of *Dicranoloma* in Australia.

Loveland's (1956) experiments were somewhat inconclusive as no sex organs appeared on spore cultures after 4 years, but all plants appeared similar to normal females, suggesting that there was no differentiation into dwarf males from sporelings. Maleness was therefore considered *not* to be genetically determined. Regeneration from excised dwarf males resulted in production of vegetative innovations when removed from female influence, suggesting some male determining inhibitory factor in females. Further evidence to support this came from spores which when grown on living female plants produced dwarf males only.

Wallace (1970), in studies on *Homalothecium megaptilum*, concluded that sex was determined at the spore stage and male dwarfism was genetically controlled, although some substance inhibiting male growth was probable, suggesting that both physiological and genetic factors might be involved. Evidence for this was derived from experiments in which dwarf plants removed from female leaves grew large although large plants in nature were rare. As differences between female and dwarf male leaves were in cell number not cell size, some factor for limiting cell division might be produced by the female.

Loveland (1956) measured spore diameter in the *Dicranum* species investigated by him but concluded that anisospory was not present. However, the graphs for *D. drummondii*, *D. bergeri*, and *D. condensatum* did show some bimodality in at least some spore populations, but the significance of this is not clear. Ramsay (1979), in studies of *Macromitrium* species, questioned the use of diameter alone as the criterion for classification of spores as anisosporous suggesting that other factors, *e.g.* wall structure and internal anatomy may be more useful in separating spores into two sexes when true dioicism is present. Olesen and Mogensen (1978) have shown differences in chloroplast structure between two sizes of spores in *Macromitrium sulcatum*. Mogensen (1981) classified a range of forms of anisospory to cover the various size range patterns that occur.

Other aspects of the cytological characteristics of mosses often ascribed to sex differentiation include presence of heteropycnotic bodies in interphase nuclei or heterochromatic segments identified by differential staining in chromosomes at early prophase stages. Cytological studies of *Dicranum tauricum* by Newton (1977) included heterochromatin banding in an effort to identify heterochromatin and its possible relationship to sex determination. A large precociously dividing heteromorphic bivalent was present in *D. tauricum* and has previously been recorded for *D. scoparium* (Briggs, 1965), *D. bonjeanii*, *D. majus* (Briggs, 1965) *D. fuscescens* and *D. scottianum* (Smith & Newton, 1968), and *D. spurium* (Anderson, 1980), although not universally present in *Dicranum* species. However, neither the H-chromosome nor the h-chromosome defined by Tatuno (1941), and referred to by Yano (1957) as heterochromatic chromosomes, regularly the largest and smallest in the complement, could be defined in the specimen studied by Newton (1977). The large chromosome was in fact devoid of any constitutive heterochromatin shown by Geimsa C-banding, and the small interphase chromacenter was shown to be derived from a medium-sized chromosome. This has opened up the whole question of whether there is any relationship between interphase heterochromatin bodies in dioicous species and sex chromosomes or sex determination. Newton (1972) had used these bodies successfully in *Mnium* species to separate the sexes, and she recognized (Newton, 1975) that a body considered as predominantly facultative heterochromatin was present in gametophytic mitotic and premeiotic interphase cells (Geimsa staining was not used).

Ramsay and Berrie (1982) have discussed the cytological and experimental evidence for mechanisms of determination in bryophytes and, Ando (1977) and Ramsay (1979) have outlined the extent of sexual dimorphism in mosses (150 species in 45 genera (Ando 1977); about one-third all moss families represented). Schellenberg (1920), Vitt (1968), Khanna (1971), Anderson (1980), and others deal with the various phenotypic forms of sexual expression in mosses. Indeed a number of possible mechanisms which result in effective dioicism can be found, *e.g.* autoicous with males and females maturing at different times, dioicism both homomorphic and hetermorphic plants, and extreme sexual differences being manifested in phyllodioicous or pseudomonoicous forms.

As the ultimate purpose of sex is effective fertilization followed by meiosis to give variation (*i.e.* in production of sporophyte in mosses) different mechanisms in different groups may be selected during evolution to achieve the same result. Phyllodiocism and pseudomonoicism have appeared randomly throughout the moss flora, occurring widely in unrelated families, but the largest numbers of examples are found in epiphytic

mosses. If the benefit of dwarfism in males is to ensure that male and female plants occur closeenough for effective fertilization (see Anderson & Lemmon (1974), Anderson (1980), Loveland (1956), and Wyatt (1977, 1982) for data on gene flow distances) then selection for such a mechanism in epiphytic mosses would increase the likelihood of fertilization when populations are isolated on separate trees some distance apart, *i.e.* with an insuperable spatial barrier to fertilization if separate isolated male and female plants were produced. The need for water and close proximity to ensure successful fertilization may be of greater importance for selection pressure in evolutionary terms than outbreeding and reassortment of genotypes. It is presumed that the dwarf males present on a female plant probably have originated from the parent sporophyte and therefore contain the same genotype, thus effectively self fertilizing the plant. It is possible, however, that even an occasional occurrence of genetically unrelated dwarf males within a population, resulting from spore dispersal from other clones, could be sufficient to maintain enough variability in the population (see Darlington, 1965; Stebbins, 1969) to outweigh the disadvantages. Meanwhile spores being dispersed will invade new territory and spread the population. The origins and relationships of the male plants on any female stem is not able to be identified until some genetic marker which distinguishes them can be found. It is thus impossible to determine which males may have originated from the parent and which invaded from separate colonies.

Preliminary studies on *Dicranoloma* have suggested the following approaches for future studies and experiments.

1. Male spores germinate and mature first, possibly inhibiting growth of female spores until the following season. Single spore cultures are needed to determine whether this is a consistent result.

2. In field collections dwarf males are found growing on a persistent protonema in the tomentum on the stem. Perhaps rather than inhibiting growth to produce dwarf males, the presence of the female encourages growth of dwarf males at the expense of female spores (a few apparent young female plants have been found). Investigations to check whether all spores germinate in presence of female extract or whether germination and development is selective should be used to check this.

3. Variability in males occurs with tall and dwarf males occurring in some populations. The males are morphologically distinct from females and tall ones produce very large numbers of perigonia and antheridia per head (20–30 compared to 5–10). The nature of differences in these different types of male plants should be ascertained.

4. Quantitative analysis of the reproductive biology of *Dicranoloma* including estimation of the relationship between occurrence of dwarf males and sporophyte production is needed.

5. Cytological investigations of more species is needed before an understanding of the cytological relationship (if any) to sexuality can be determined.

Cytologically *Dicranum* and *Dicranoloma* have similar characteristics in chromosome numbers recorded and chromosome behavior even though only a small proportion of species from a limited area have been investigated, 4% of Australian *Dicranoloma* species, 17% of *Dicranum* species. These preliminary studies show differences in karyotype between species and between genera which should be investigated further. Whether these differences reflect or support generic separation is not yet assessable.

More extensive and intensive cytotaxonomic and experimental studies of factors

initiating gametangia in taxa in which sexual dimorphism occurs in mosses should be carried out to ascertain the control mechanisms involved in sex determination. *Dicranum* and *Dicranoloma* are genera in which such studies are likely to be profitable.

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APPENDIX 1: Details of voucher specimens for *Dicranoloma*.

Data are presented here for all populations of *Dicranoloma* for which this information has not previously been published. This includes (a) the present paper (b) Ramsay & Berrie (1982) see*). Collection details for Ramsay (1967, 1974) were given with chromosome numbers in Ramsay (1967), but cytological characteristics are dealt with in the present paper. Note: names are tentative awaiting a revision of the genus in Australia, particularly *D. robustum*, *D. billardieri* and *D. serratum*.

Dicranoloma menziessi (Hook.f. & Wils.) Par.

Chromosome studies

34/79	Mt. Wilson N.S.W. Australia H. Ramsay 6 Oct. 1979 meiosis $n=8$
31/80	Zircon Creek Mt. Wilson N.S.W. Australia A. Murray 25 Nov. 1980 meiosis $n=8$

Other studies (C = cultures, S = spore cultures, ♂ dwarf males; other specified, T = time culture kept)

*80081	Wauchope N.S.W. A. Murray 1 Aug. 1980 [C(S) (T = 5 months)]
*801125	from 31/80 C(♀, stems, ♀ leaf) T = 3–6 months
80481-3	Wauchope N.S.W. Australia A. Murray 20 July 1980 [C(S, ♂, leaf ♀ T = 9 months)]

Dicranoloma dicarpum (Nees) Par.

Chromosome studies

15/80	Mt. Allyn Chichester State Forest N.S.W. Australia. A. Bishop 17 Aug. 1980 meiosis $n=7$

Other studies

*801881	(see 15/80 above) [C(S; ♂; ♂ with ♀ leaves) T = 22 months)]
*80178	Wauchope N.S.W. Australia A. Murray 17 Aug. 1980 [C (S; ♂; leaves; ♀; with ♂) T = 21 months]
*8081	Allyn R. Chichester State Forest N.S.W. Australia A. Bishop 17 Aug. 1980 (studies dwarf males, distribution on ♀)

Dicranoloma billardieri (Brid.) Par.

Chromosome studies

12/80	Megalong Valley Blackheath N.S.W. Australia H. P. Ramsay 2 Aug. 1980 meiosis $n=12$
14/80	Megalong Valley Blackheath N.S.W. Australia H. P. Ramsay 2 Aug. 1980 meiosis $n=12$

Other studies

*812331	Mt. Wilson N.S.W. Australia H. P. Ramsay 26 Mar 1981 [C (♂, stem fragments) T = 15 months)]
801	Megalong Valley Blackheath N.S.W. Australia (dwarf male distribution on females)

Dicranoloma serratum (Broth.) Par.

Chromosome studies

28/79	Mt. Banda Banda Wauchope N.S.W. Australia A. Murray 16 June 1979 meiosis $n=9(7+2m)$
4/76	Mt. Wilson N.S.W. Australia H. P. Ramsay 13 Jan. 1976 meiosis $n=8(7+m)$

Other studies

*7613	Mt. Wilson N.S.W. Australia H. P. Ramsay 13 Dan. 1976 counted dwarf males per female
812331	Mt. Wilson N.S.W. Australia H. P. Ramsay 26 Mar. 1981 [C(♂, leaf, stem) T = 15 months]

Dicranoloma robustum (Hook f. & Wils.) Par.

Chromosome studies

24/82	Barrington Tops N.S.W. Australia J. Bruhl 7 Aug. 1982 meiosis $n=7$

Other studies

*75191	Bulls Head A.C.T. Australia H. P. Ramsay 19 Jan. 1975 (dwarf males, distribution on females)
8121011	Katoomba N.S.W. Australia H. P. Ramsay 21 Jan. 1981 [C(♂, leaves) T = 6 months]

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THE STRUCTURE AND SIGNIFICANCE OF THE LEUCOBRYACEOUS LEAF[1]

HAROLD ROBINSON[2]

Abstract. The characteristic leucocyst-chlorocyst cellular pattern in the moss family Leucobryaceae depends functionally on the presence of air inside the leaf. Such leaves prove basically different in structure and function from those of other mosses, including the leucocyst-containing *Sphagnum*. The family Leucobryaceae is redelimited to include eight genera, *Leucobryum*, *Arthrocormus*, *Cladopodantus*, *Holomitriopsis*, *Ochrobryum*, *Octoblepharum*, *Schistomitrium*, and *Steyermarkiella*. The genera *Exodictyon* and *Leucophanes* are transferred to the Calymperaceae. A fossil of *Octoblepharum* in amber is cited, showing trapped air in the leaves.

The family Leucobryaceae is widely distributed in the temperate and tropical regions of the world and is most noticeably different from most other mosses by the pale whitish aspect of the plants, after which the typical genus *Leucobryum* is named. Under the microscope, the leaves of the Leucobryaceae show distinction from other mosses in the enlarged hyaline cells (leucocysts) in two or more layers, enclosing a reticulum of narrow chlorophylliferous cells (chlorocysts) usually in a single central layer. These characteristics make the family one of the most easily distinguished among the mosses, but they raise interesting questions as to how such leaves function and as to their evolutionary source.

As treated by Brotherus (1924), the Leucobryaceae included nine genera, *Ochrobryum* Mitt., *Schistomitrium* Dozy & Molk., *Cladopodanthus* Dozy & Molk., *Leucobryum* Hampe, *Leucophanes* Brid., *Cardotia* Besch., *Octoblepharum* Hedw., *Arthrocormus* Dozy & Molk., and *Exodictyon* Card. *Cardotia* has since been synonymized with *Leucobryum* by Andrews (1947), *Carnifolium* has been described by Williams (1931) and synonymized with *Octoblepharum* by Bartram (1960), and two genera, *Holomitriopsis* and *Steyermarkiella*, have been named by Robinson (1965*b*). The genera represent considerable diversity in detailed structure, and a number of authors such as Fleischer (1904), Herzog (1926), and Andrews (1947) have considered the family to be polyphyletic, being partly related to the Dicranaceae and partly to the Calymperaceae. Even with such a double origin, the leucobryaceous leaf design is of restricted distribution in the mosses, being found only in members of the haplolepideous series. For some reason, the leaf type has not been attained by other groups of mosses, though the Leucobryaceae are common enough to indicate that the leaf design must be of some evolutionary value. The

[1]Acknowledgements. Scanning electron microscope negatives were taken in the SEM Laboratory at the Smithsonian Institution supervised by Walter Brown. The Coates and Welter field emission microscope was operated by Susan Braden. Other photographs for the paper were prepared by Victor Krantz, Staff Photographer, National Museum of Natural History. The study has been aided by Clyde F. Reed of Baltimore and Deborah Bell of the National Herbarium staff, who have collected some fresh material during local trips.

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restriction would lead one to believe that there is some unsuspected complexity involved in what seems a rather simple leaf form.

In one respect, the leucobryaceous leaf is not unique. The Sphagnaceae also have a basic leaf pattern of large hyaline cells or leucocysts and a reticulum of narrow chlorocysts. The Sphagnaceae are basically different in most other respects, however. They have their two leaf cell types in a single layer, and the two cell types represent a differentiation within that layer; a differentiation within the products of each final set of cell divisions within that layer. The pores in the leucocysts in the leaves of *Sphagnum* open to the outside rather than into neighboring leucocysts. Finally, the chlorocysts of *Sphagnum* are usually partly exposed to the outer surface of the leaf, rarely being slightly removed from the outer surface (included) as in *S. magellanicum* Brid. or *S. compactum* DC. These characteristics are in plants that seem specialized for boggy habitats and which are well known for their water-holding capacity. The structures of the Sphagnaceae seem developmentally rather complex but functionally simple and serve to emphasize the remote systematic position of their ancient lineage among the mosses.

The Leucobryaceae, in contrast, inhabit more mesic localities, have comparatively little water-holding capacity, have cells in more than one layer with the chlorocysts completely enclosed, and in their typical form have pores restricted almost completely to the walls between the leucocysts rather than the outer walls. The number of contrasting features between the Sphagnaceae and Leucobryaceae would suggest that, in spite of the superficial similarity in cellular differentiation, the two are not only systematically remote, but also functionally different.

It was a functional consideration regarding the leucobryaceous leaf that initially led to the present study, the question of how a series of chlorocysts buried in the center of a multistratose leaf could adequately exchange gasses for photosynthesis. It was thought that the leucocysts of the Leucobryaceae and possibly the Sphagnaceae would enhance photosynthesis by having air bubbles mixed with the water in the cells. Such bubbles are commonly seen in remoistened herbarium material, and their presence in living material could easily be ignored by any bryologist who was not looking for them. For this reason, a few members of the Sphagnaceae and Leucobryaceae have been observed in the living condition, revealing a further basic difference between the two families.

In the specimens of live *Sphagnum* examined, there was no air in the leucocysts. The material involved was from emergent branches, fully exposed to the air, but showed no sign of excessive drying that is sometimes experienced by living plants in nature. In living *Sphagnum imbricatum* Hornsch. ex Russ., not only were the leucocysts filled with water, but the chloroplasts were aligned almost exclusively along the one of the three walls of the chlorocysts that is exposed to the surface of the leaf. This would indicate that most of the photosynthesis in the chlorocysts is in the part most exposed to the air.

In the specimens of *Leucobryum*, air is present in the leucocysts of the leaf, usually in the form of large bubbles that extend through many cells. Such bubbles are either adaxial or abaxial to the chlorocysts, or on both sides. The young leaves, as they enlarge, show the development of air pockets, while older leaves that seem to be non-functional evidently lose their air. In the basal parts of the plant, the leucoysts are apparently converted to a water-holding function. On the basis of these observations, it would seem that a large part of the "leuco" in *Leucobryum* is caused by the air bubbles. In spite of the small sample seen, the presence of air in the leaf is assumed to be characteristic of the

Leucobryaceae, since their structure would seem to require such a specialization in order to properly photosynthesize.

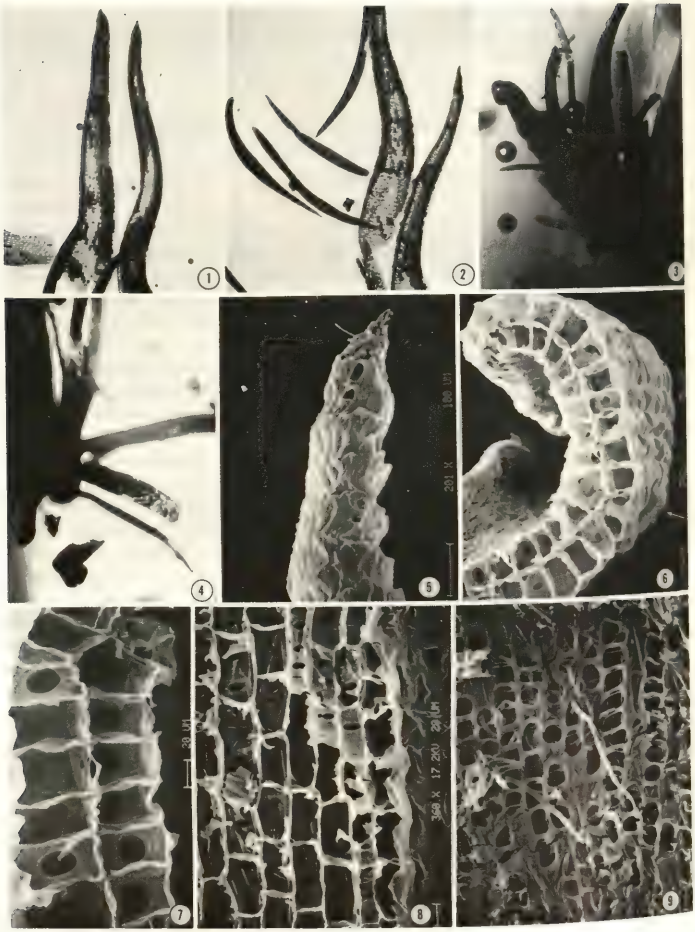
It seems that the most significant complication in the evolution of the Leucobryaceae has been the ability to produce and maintain the air bubbles in the leaves. Such bubbles are necessary for the function of the chlorocysts, which are remote from the surface of the leaf, and which could not properly exchange gases if the leucocysts were all filled with water. Such a complication would explain why such a specialization has not occurred more widely, but it remains to be considered why the specialization has occurred at all.

In land plants generally, the more evolved forms seem to devise some means to trap air in small spaces adjacent to photosynthesizing cells. In most mosses this is achieved crudely by imbrication of the leaves. In vascular plants, in moss capsules, and in many Marchantiales, this is achieved by development of an internal spongy mesophyll or its equivalent connected to the outside by stomata or stomata-like openings in the epidermis. In most Polytrichaceae and some Pottiaceae in the mosses, air is trapped among closely packed lamellae or filaments on the upper surface of the costa, sometimes aided by the infolded margins of the leaves. The Leucobryaceae seem to present an additional model, with air trapped inside of the cells adjacent to the photosynthesizing cells. In such protected positions in the plants, the walls of the photosynthesizing cells are probably able to be structurally specialized and can be maintained with an optimum amount of moisture for gaseous exchange.

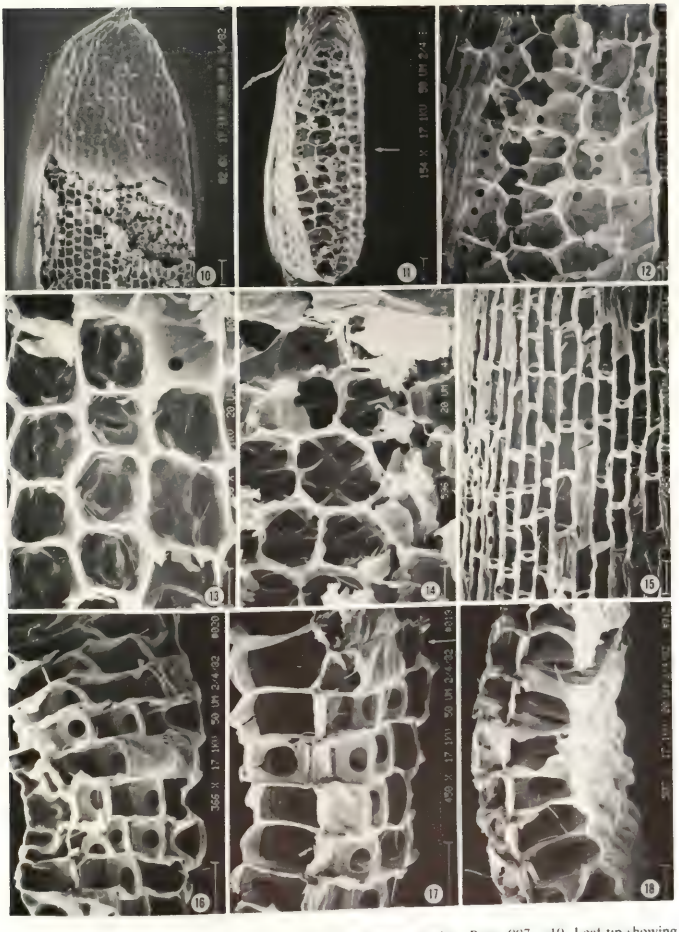
The detailed structure of the Leucobryaceous leaf has been examined with the scanning electron microscope (Figs. 5–27). In spite of variation in detail, most of the genera of the family, including *Leucobryum, Arthrocormus, Cladopodanthus, Holomitriopsis, Ochrobryum, Octoblepharum, Schistomitrium*, and *Steyermarkiella*, seem to share similar tendencies in structure of the outer surface, the midline of the leaf, and the distribution of pores in the leaf. In many of the views, the weak walls of the chlorocysts have collapsed, and those cells cannot be distinguished.

Study of the above generic series seems to support the view of Lorch (1894) that the thickened part of the Leucobryaceous leaf is an expanded costa. The structure across the width of the multistratose part is uniform except for the minor but characteristic aberration in cell alignment along the midline (Figs. 6–7, 11, 17, 19). In no case are any cells except leucocysts and chlorocysts present, even in *Arthrocormus* (Figs. 23–25). In most cases the chlorocysts extend across the multistratose portion in a single median layer. In *Arthrocormus* the chlorocysts are in two layers below with a partial third layer in the upper part of the leaf (Figs. 23–25). The chlorocysts are usually at the intersections of four cells in *Leucobryum* (Figs. 6–7), *Holomitriopsis* (Figs. 17–18), *Arthrocormus* (Figs. 23–25), and in most other genera of the series. The chlorocysts seem characteristically at the intersections of three cells in *Octoblepharum* (Fig. 11) and *Steyermarkiella* (Figs. 19–20).

In the above series of genera, the outside walls of the leucocysts are usually completely without pores, and this is assumed to be a basic feature of the leaves of the group. Breakage is common in some preparations, however, and it is possible that most leaves have some broken outer walls in nature. There are indications that some members of the family have partially reverted from the basic functional design as in the case of *Holomitriopsis* (Figs. 15–17). In this genus, the breakage of the outer walls on the abaxial leaf surface is so extensive that it must be true of the living leaves, and the chlorocysts are evidently partially exposed to the air in this way. It is notable that the walls on the adaxial



FIGURES 1–9. Leucobryaceae.—1–2. Leaves of living *Leucobryum glaucum* (Hedw.) Ångstr. containing air in leucocysts, × 14.—3–4. *Octoblepharum* sp. in amber, showing included air, × 10.—5–6. *Leucobryum scalare* C. Müll. ex Fleisch., *Touw 10293*.—5. Leaf tip, line 100 µm.—6. Cross section, line 50 µm.—7–9. *L. glaucum*, *Lorch*, 13.5.1925.—7. Cross section, line 20 µm.—8. View of cut surface showing three layers of walls from outer to the chlorocyst level, line 20 µm.—9. Leaf base showing resorbed outer surfaces of leucocysts, line 20 µm.



FIGURES 10–18. Leucobryaceae.—10–14 *Octoblepharum albidum* Hedw., *Reese 907*.—10. Leaf tip showing outer surface and shaved portion, line 100 μm.—11. Cross section, line 50 μm.—12. Longitudinal section near tip, line 20 μm.—13–14. Leaf interior showing cell walls between chlorocysts and some overlying pericinal tip, line 20 μm.—15–18. *Holomitriopsis laevifolia* (Broth.) H. Robins., *Steyermark 92613*.—15. Abaxial walls, line 20 μm.—15–18. *Holomitriopsis laevifolia* (Broth.) H. Robins., *Steyermark 92613*.—15. Abaxial walls, line 20 μm.—16–17. Cross sections showing abaxial surface, lines 50 μm.—18. Cross section leaf surface, line 50 μm.—16–17. Cross sections showing abaxial surface, lines 50 μm.—18. Cross section showing adaxial surface, line 20 μm.

surface of the leaf remain intact (Fig. 18) and that air bubbles probably occur on that side of the leaf. In this regard, it seems significant that the adaxial leucocysts in *Holomitriopsis* are much larger than those of the abaxial surface. This feature was noted by Florschütz (1964) when he suggested the South American species are related to the Malaysian genus *Schistomitrium* which has similar leaf structure. The relationship has since been confirmed by discovery of a sporophyte, though separate generic status has been established on the basis of the calyptra (Robinson, 1965*b*). Both genera occur in extremely moist areas of the world, where the plant would be served best by leaving the chlorocysts exposed abaxially to the moist air.

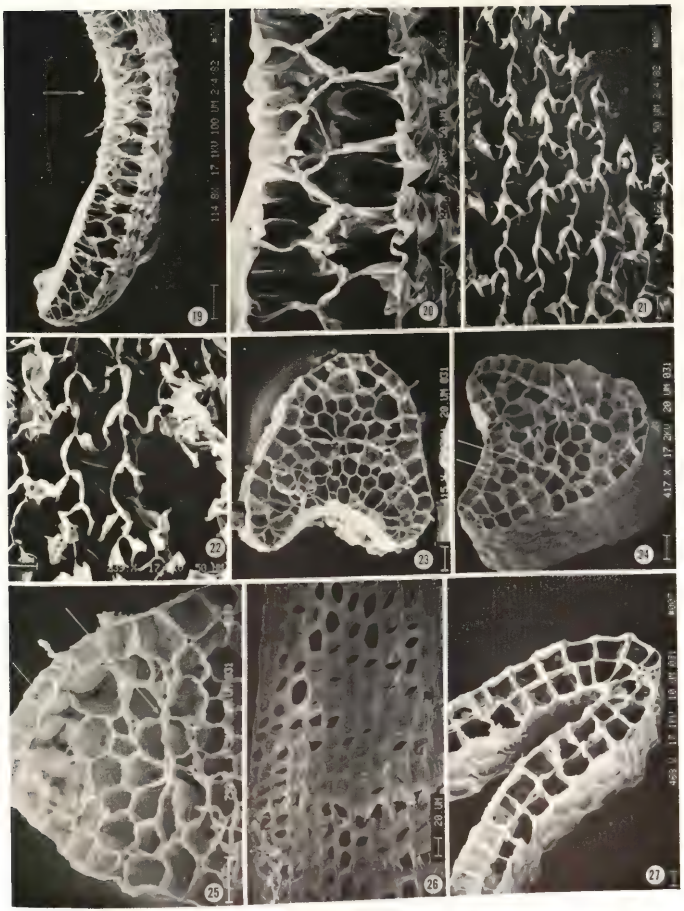
In *Leucobryum* (Fig. 9), the outer walls of the leucocysts in the leaf base are extensively resorbed, but the exposure to the air is limited by the manner in which the leaf bases are closely appressed. Also, such openings are remote from the parts of the leaf where air bubbles are most concentrated. The openings near the leaf base seem more likely to provide entry for water than for air. The outer walls of the leucocysts in *Leucobryum* and other members of the family are usually flat or slightly bulging, but they form projecting points in some Asiatic species such as *Leucobryum scalare* C. Müll. ex Fleisch. (Fig. 5).

The distribution of pores within the leaf shows some interesting variations in the series of genera listed above. The walls lying in the plane of the leaf, connecting the chlorocysts, seem basically different in structure, and they usually lack pores (Figs. 12–15, 17, 21). This is also true of the cells running between the chlorocysts in each of the three layers of the *Arthrocormus* leaf (Fig. 25). The principal exception seems to be in *Leucobryum* (Figs. 7–8), but even there, the walls between the chlorocysts have pores less developed or sometimes lacking. The effect of this restriction of pores is seen in living material where the air bubbles of the two surfaces of the leaf seem to function independently of each other.

Other cell walls in the interior of the leaf usually have pores. In cases where there are more than two layers of leucocysts, the periclinal walls lying in the plane of the leaf show no differentiation from the transverse or vertical walls, and they contrast with the underlying walls between the chlorocysts (Figs. 8, 13). The same basic differentiation between walls with pores and those without them is seen in the more complex leaf of *Arthrocormus* (Fig. 25).

The greatest divergence from the conventional pattern of pores in the leucobryaceous leaf seems to be in *Steyermarkiella*. In the latter genus, the pores are almost completely restricted to the transverse walls, which protrude downward into the adjacent cells (Figs. 21–22). The pattern of specially shaped cells is most evident in the median part of the leaf. The intrusive cell type is distinct from forms in all other Leucobryaceae, but it is reminiscent of the form of the cortical cells in the stems of *Sphagnum portoricense* Hampe. Because of the restricted distribution of the pores in *Steyermarkiella*, it would seem that air bubbles in the leaves would often be limited to individual files of cells. Such a pattern of air bubbles could create a distinctive reflectance pattern in the living leaves, which would be visible to collectors. The evolutionary value of the specialized leaf form of *Steyermarkiella* is questionable, in view of the restricted endemism of the single species in the eastern Guayana Highlands of Venezuela.

A number of the foregoing genera share many characteristics of the Dicranaceae, and, as recognized by Cardot (1900), they seem to relate to such genera of the Dicranaceae as *Campylopus* Brid., *Brothera* C. Müll., and *Paraleucobryum* (Limpr.) Loeske. There



FIGURES 19–27. Leucobryaceae and *Leucophanes*.—19–22. *Steyermarkiella anomalodictya* H. Robins., *Steyermark 92266*.—19–20. Cross sections.—19. Line 100 μm.—20. Line 50 μm.—21–22. Shaved leaves showing median cells, lines 50 μm.—23–25. *Arthrocormus schimperi* (Dozy & Molk.) Dozy & Molk., *Leiberg 122*, cross sections, lines 20 μm.—25. Tilted to show vertical walls.—26–27. *Leucophanes candidum* (Schwaegr.) Lindb., *Hale & Banaag 24512*.—26. Leaf surface showing resorbed outer walls of leucocysts, line 20 μm.—27. Cross section showing area of complete outer walls and stereid band, line 10 μm.

remain two genera that have been placed in the Leucobryaceae that are very anomalous and that show more relationship to the Calymperaceae.

Exodictyon is structurally most similar to the Calymperaceae, with surviving narrow laminae, which extend nearly to the leaf tip. The laminae have unique fenestrations or narrow outliers of the basal cancellinae, each with a few leucocysts in a single series. Still, the mass of the leaf tissue is in the form of an enlarged and fleshy costa, which closely resembles in shape the leaf of *Arthrocormus*. It is in the latter genus that most of the original species of *Exodictyon* once resided. The important difference is that the chlorocysts of *Exodictyon* are not inside the costa but in a reticulum on the surface. From the appearance of the material seen in this study under the light microscope, it is unlikely that the small guide cells in the center of the costa actually contain chlorophyll. The structure seen in *Exodictyon* has no functional need of internal air pockets, and the genus has no specialization that would suggest that such pockets occur. In spite of the similarity in leaf shape, *Exodictyon* seems to have no close relationship to *Arthrocormus*, which has internal chlorocysts.

Leucophanes also shows evident relationship to the Calymperaceae, but it has leucocysts and chlorocysts positioned as in *Leucobryum* rather than as in *Exodictyon*. *Leucophanes* differs from other Leucobryaceae in having remnants of one or two stereid bands at the midline of the leaf as shown by Cardot (1900) and in Figure 27. Also, in the leaf shape and differentiated margin, the leaf of *Leucophanes* resembles an ordinary lamina of a moss leaf and, unlike the non-unistratose parts of other leucobryaceous leaves, was regarded as a lamina by Lorch (1931). Detailed examination shows one difference from most Leucobryaceae that is of functional importance: the leucocysts seem commonly resorbed on their outer surfaces (Fig. 26). Although some areas of leucocysts remain enclosed (Fig. 27), there are areas in various parts of the leaf where the leucocysts are open on all their walls. Some pores in the central walls are visible in the leaf section (Fig. 27). It is questionable whether internal air pockets would be produced and maintained in *Leucophanes* in the same way that they are in typical Leucobryaceae. Except for the fact that they enclose chlorocysts, there is no particular difference between the leucocysts of *Leucophanes* and the cells of the cancellinae that are present in the bases of the leaves of most Calymperaceae.

In spite of the differences in detail, *Leucophanes* remains sufficiently similar to most other Leucobryaceae to give the impression of a continuum. Since the two related families, Dicranaceae and Calymperaceae, do not seem particularly close to each other, there is a phyletic problem. Cardot (1900) resolved the double relationship of the family by suggesting that the Leucobryaceae was ancestral, with the Dicranaceae and Calymperaceae derived. The latter families would presumably be reversions to the more normal moss form. Andrews (1947) referred to Cardot's idea as " . . . obviously an inversion of the evolutionary process."

Authors who have concerned themselves with the relationships of the Leucobryaceae all seem to have recognized the calymperaceous relationship of *Leucophanes*, although they have often treated the genus in a separate family, Leucophanaceae. Herzog (1926) alone seems to have placed only *Leucophanes* in the latter family, while Fleischer (1904) included *Cardotia, Octoblepharum, Arthrocormus*, and *Exodictyon*. It is notable that most, but not all, of the genera included by Fleischer have some irregularity in leucocyst positions that results in some or all the chlorocysts' being traingular. In placing

Leucophanes, Arthrocormus, Exodictyon, and *Octoblepharum* in the Calymperaceae, Andrews (1947) seemed to follow Fleischer rather closely, but Andrews cited the reduced "Pottioid" peristomes of some of the genera, and the calymperaceous type of propagula on the leaf apices of such genera as *Exodictyon, Leucophanes*, and *Octoblepharum*. Both of the latter characters are of doubtful value, however, especially the propagula. Such propagula are also found on the leaves of *Ochrobryum*, which was placed in the Dicranaceous group by Andrews. The reduced peristome is probably only a by-product of the erect capsule form that is widespread in the family. Erect capsules occur in most of the genera of the family except *Leucobryum*, and they even occur in one species of that genus (*L. incurvifolium* C. Müll.; Robinson, 1965*a*).

The present effort to resolve the polyphyletic nature of the Leucobraceae benefits from one additional insight. Although a leucocyst-chlorocyst leaf structure has evidently evolved more than once, it seems possible that forms dependent on internal air pockets in the leaf evolved only once. On this basis, two of the genera seem separable from the rest as lacking all the specializations that would require such internal air bubbles. The two genera, *Exodictyon* and *Leucophanes*, are the same ones that show the greatest discontinuity of structure from the typical Leucobryaceae, and they are the same two that show clear evidence of relationship to the Calymperaceae.

The remaining genera are considered here as relatives of the Dicranaceae, where *Brothera, Campylopus*, and *Paraleucobryum* show some cellular structure in the leaves closely approximating that of the Leucobryaceae. It seems likely that at least some of these Dicranaceae, especially some species of *Campylopus*, will prove to have air inside of the large cells of their leaves. Andrews (1947) and Robinson (1971) have gone so far as to include the typical element of the Leucobryaceae in the Dicranaceae, but there seems to be little acceptance of such a treatment. It seems best, at present, to retain the family Leucobryaceae, minus *Exodictyon* and *Leucophanes*, as a probably monophyletic though closely related derivative of the Dicranaceae.

As a final note, fossil material of the Leucobryaceae has been seen in a piece of amber owned by Francis M. Hueber of the Department of Paleobiology in the National Museum of Natural History. The amber from the Dominican Republic dates generally from the Oligocene-Miocene boundary, twenty to twenty-five million years ago. The included moss is unquestionably an *Octoblepharum* with a form that could have been ancestral to both the typical and *Carinafolium* types in the genus (Figs. 3–4). The specimens were supposedly immersed in the resin while in the living condition, so that it is of interest that the leaves of the fossil show included air. Such air is absent in other bryophyte fragments seen in the amber.

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A NATURAL HYBRID BETWEEN *BRUCHIA MICROSPORA* NOG. AND *TREMATODON LONGICOLLIS* MICHX.[1]

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Abstract. Two types of morphologically distinct sporophytes were observed to occur on *Bruchia microspora* gametophytes. One is immersed, typically cleistocarpous, and 93% of the spores contain cytoplasm. The second sporophyte type exhibits intermediate characteristics between *Bruchia microspora* and *Trematodon longicollis*. It has a fragmentary peristome, a well-defined but nonfunctional annulus region, and only six percent of the spores contain cytoplasm. Quantitative and qualitative analyses of the sporophyte morphology of the two sporophyte types produced on *Bruchia microspora* support the hypothesis that intergeneric hybridization occurs between these two genera. The hybrid sporophyte is designated by the formula *Bruchia microspora* Nog. ♂ × *Trematodon longicollis* Michx. ♂. The type specimen and the protologue for *Bruchia microspora* Nog. include both types of sporophytes. A lectotype is provided for *Bruchia microspora*, and the original description of the sporophyte of the latter is emended to exclude the hybrid sporophyte.

A recent proposal (Buck, 1979) recommends the restoration of the moss genus *Bruchia* and its allied genera, *Trematodon, Pringleella* and *Eobruchia*, to the family Bruchiaceae. A major portion of the discussion concentrates on justifying a close relationship between the normally cleistocarpous, aperistomate genus *Bruchia* and the stegocarpous, peristomate genus *Trematodon*. Despite the existing uncertainty as to whether *Bruchia* and its allies belong in the Ditrichaceae, the Bruchiaceae or the Dicranaceae, it is generally acknowledged that *Bruchia* and *Trematodon* are, indeed, closely related (Brotherus, 1909, 1924; Britton, 1913, Grout, 1936; Takaki, 1962; Scott et al., 1976; Smith, 1978; Crum & Anderson, 1981; Corley et al., 1981). Further evidence to support the close relationship between the two genera is available. Bryan (1956) has demonstrated that *Bruchia* and *Trematodon* exhibit remarkably similar cytological features. They are similar in their chromosome number, show a similar characteristic chromosome behavior during meiosis, and react similarly to methods of preparation. A report by Iwatsuki and Mizutani (1972) that a rudimentary peristome occasionally develops in the capsules of the otherwise cleistocarpous *Bruchia microspora* is especially noteworthy in view of the fact that the type collection is reported to contain a mixture of *Bruchia* and *Trematodon* (Noguchi, 1951). These observations, when taken into consideration with our recent discovery that all collections of *Bruchia microspora* in which a rudimentary peristome is produced also contains a mixture of *Trematodon*, suggests to us that hybridization might be occurring between the two genera.

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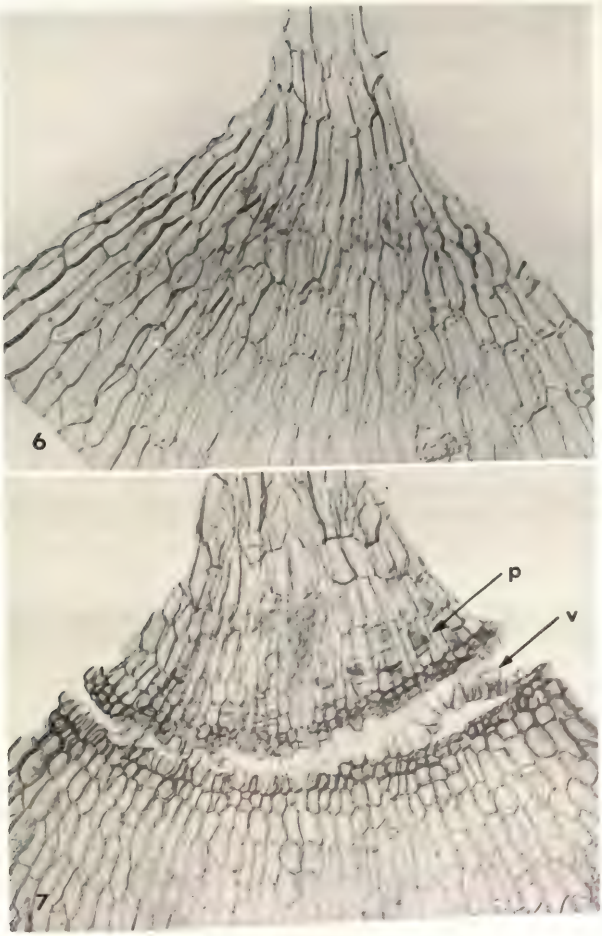
FIGURES 1–5. Habits of putative hybrid and parents.—1–2. *Bruchia microspora* with normal sporophyte (×6).—3–4. *Bruchia microspora* with hybrid sporophyte. Arrow denotes normal sporophyte growing on same gametophyte as hybrid sporophyte (×6).—5. *Trematodon longicollis*, male parent (×3).

Bruchia microspora Nog. is a rare species endemic to the island of Kyushu, Japan. The taxon was described by Noguchi (1951) based on a mixed collection also containing *Trematodon longicollis* Michx. An extensive herbarium search, initiated in conjunction with a generic revision of *Bruchia* by the first author, has uncovered only six collections of this species. All six specimens, including the type, were collected in Kumomoto Prefecture by K. Mayebara. The type was collected in May, 1936; the remaining five collections were gathered during March and April, 1952. All of the collections contain *Bruchia microspora* mixed with *Trematodon longicollis*.

A close examination of these collections (19 packets) has revealed that a mixture of two kinds of sporophytes with distinctly different morphologies occur on morphologically identical *Bruchia* gametophytes. One of the sporophyte types is typically *Bruchia*-like in its morphology (Figs. 1–2). The capsule is immersed on a short, thin seta, has a short neck and rostrum, and is completely cleistocarpous with no trace of an annulus or a peristome (Fig. 6). The second kind of sporophyte (Figs. 3–4) exhibits a morphology intermediate between the immersed, cleistocarpous sporophyte and the long-exserted, stegocarpous, peristomate sporophyte of *Trematodon longicollis* (Fig. 5). The capsule is shortly exserted on a longer, thicker seta and has a well-developed neck and a longer rostrum. Statistical analyses of quantitative sporophyte features of the two types of *Bruchia microspora* sporophytes and *Trematodon longicollis* are summarized in Table 1.

The capsule of the intermediate sporophyte occurring on *Bruchia*, when mounted and cleared in Hoyer's medium, exhibits a surprisingly well-developed annulus region comprised of one to two rows of short, rectangular exothecial cells surrounded above and below by a row of thick-walled quadrate cells (Fig. 7). A single row of vesiculose cells



FIGURES 6–7. Annulus region of *Bruchia microspora* capsules.—6. Undifferentiated region of normal, cleistocarpous capsule (×175).—7. Differentiated annulus region of hybrid sporophyte showing portion of inner row of vesiculose (V) cells and rudimentary peristome (P) remaining attached to "operculum" (×175).

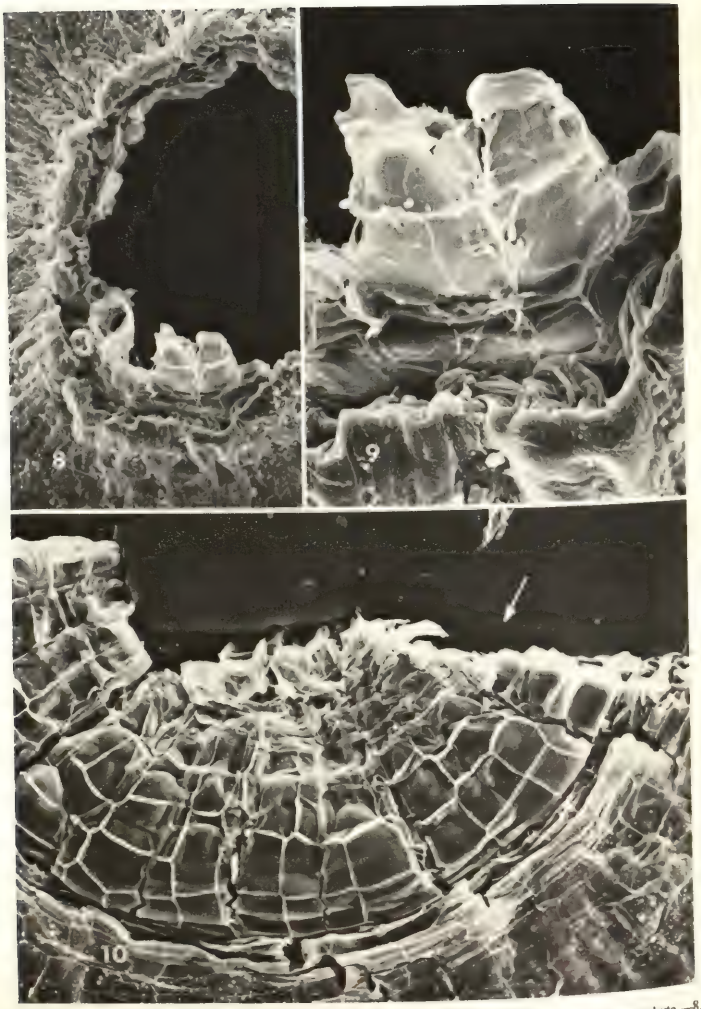
TABLE 1. Statistical data comparing thirteen sporophyte characteristics from selected population samples of *Bruchia microspora* normal sporophyte (B), intermediate sporophyte between *Bruchia microspora* and *Trematodon longicollis* (B × T) and *Trematodon longicollis* sporophyte (T).

Character	Taxon	Mean	Range	Std. dev.	Std. error	Coeff. of Variation	Sample size (n)
Seta length (mm)	B	0.78	0.65–1.04	0.14	0.05	18.4	9
	B × T	1.82	1.20–2.42	0.36	0.11	20.0	11
	T	18.55	16.51–24.21	3.20	1.43	17.3	5
Seta width (mm)	B	0.16	0.14–0.18	0.01	0.004	7.3	9
	B × T	0.19	0.16–0.22	0.02	0.005	9.5	11
	T	0.15	0.12–0.18	0.03	0.013	20.0	5
Capsule length (mm)	B	1.31	1.10–1.51	0.13	0.04	10.0	9
	B × T	1.71	1.59–1.90	0.10	0.03	13.6	11
	T	8.61	7.29–9.70	0.96	0.43	11.2	5
Rostrum length (mm)	B	0.33	0.26–0.39	0.04	0.01	12.1	9
	B × T	0.37	0.29–0.44	0.05	0.02	13.6	11
	T	1.43	1.30–1.64	0.14	0.06	9.9	5
Spore sac length (mm)	B	0.71	0.60–0.83	0.09	0.03	12.3	9
	B × T	0.77	0.65–0.88	0.07	0.02	8.6	11
	T	2.34	1.90–2.83	0.34	0.02	14.5	5
Neck length (mm)	B	0.27	0.18–0.36	0.05	0.02	18.0	9
	B × T	0.58	0.42–0.70	0.09	0.03	15.7	11
	T	4.84	4.01–5.38	0.54	0.24	11.1	5
Capsule length from widest point to tip (mm)	B	0.71	0.60–0.83	0.08	0.03	10.7	9
	B × T	0.78	0.65–0.88	0.06	0.02	8.3	11
	T	2.61	1.82–3.20	0.56	0.25	21.5	5
Capsule length from widest point to base (mm)	B	0.60	0.47–0.78	0.10	0.01	16.6	9
	B × T	0.94	0.78–1.12	0.11	0.03	11.5	11
	T	6.00	4.94–6.63	0.70	0.31	11.6	5
Capsule width at widest point (mm)	B	0.55	0.49–0.60	0.03	0.01	6.3	9
	B × T	0.61	0.52–0.73	0.05	0.02	8.8	11
	T	0.73	0.65–0.81	0.06	0.03	8.5	5
Neck base width (mm)	B	0.23	0.21–0.26	0.01	0.04	5.6	9
	B × T	0.29	0.23–0.34	0.03	0.01	11.7	11
	T	0.26	0.21–0.31	0.04	0.13	16.8	5
Spore diameter (μm)	B	30.28	28.36–32.03	1.20	0.41	4.0	90
	B × T	24.98	22.85–26.52	1.13	0.34	4.5	110
	T	22.36	21.62–22.85	0.53	0.24	2.4	50
Capsule exserted above leaf (mm)	B	–0.63	–1.20—0.31	0.27	0.09	–42.4	9
	B × T	3.53	2.79–4.21	0.43	0.13	56.0	11
	T	24.07	22.23–29.33	2.98	1.33	12.4	5
Sporophyte length (mm)	B	2.08	1.79–2.50	0.26	0.09	13.5	9
	B × T	3.53	2.79–4.21	0.43	0.13	12.1	11
	T	27.16	25.22–32.58	3.09	1.38	11.4	5

(Fig. 7), suggesting a revoluable annulus similar to that produced by *Trematodon*, is formed in the cell layer immediately internal to the differentiated exothecial cells. The vesiculose cells are observed only upon rupturing of the differentiated exothecial cell layer. The annulus region can be discerned as a faint red line occurring immediately below the rostrum in older capsules. The annulus is apparently non-functional in nature, as we were unable to observe any sporophytes in which the "operculum" became separated

from the urn. Immediately above and internal to the annulus region we detected traces of a short, fragmentary peristome consisting of sixteen teeth (Figs. 7–10). Attempts to remove the "operculum" to expose the peristome were generally unsuccessful as the teeth remain attached to the inner surface of the "operculum." Occasionally, in very old capsules, a few teeth would remain attached to the mouth of the urn (Figs. 8–9). The dorsal surface of each tooth of the peristome is formed by a single row of cells (Fig. 9). The ventral surface is developed from two rows of cells as evidenced by the irregular median line formed along each tooth (Fig. 10). This is the pattern observed in the development of a haplolepidous peristome. The median line and the irregular deposition of thickened material contributing to the ventral surface of the teeth terminate approximately four cells from the base of the peristome and can be discerned as a faint horizontal ridge (Fig. 10, arrow).

Additional morphological evidence to support the hybrid origin of the peristomate sporophyte is provided from analyses of spore features. All of the peristomate capsules produced spores which were intermediate in size and structure to those of the putative parents. The spores of *Bruchia microspora* have distinct proximal and distal surfaces and range in diameter from 24–32 μm. The distal surface is covered with spinae which are sometimes fused (Fig. 11). The aperture region of the proximal surface is surrounded by rows of spinae forming a triangular outline, the annulus. Surrounding the annulus are two collars. The first collar is smooth to sparsely verrucate and is delimited by a ring of spinae, many of which are fused; the second is usually smooth and is also delimited by a ring of fused spinae (Fig. 11). The spores of *Trematodon longicollis* were described by McClymont (1954) as having a well-defined triangular aperture surrounded by a ring of somewhat anastomozing spinae-baculi and two collars separated by a ring of spinae-baculi. The spores of the Japanese material used in our study range in size from 21.6–22.8 μm. The proximal and distal surfaces are typically distinguishable (Fig. 12), but the annulus is not well-defined. The distal surface is covered by baculi which are blunt-tipped. The aperture region of the proximal surface is surrounded by baculi which form an indistinct triangular annulus. The first collar is densely covered with spinae-baculi. Brown and Lemmon (1981) found that the annulus in the mature spores of *T. longicollis* is covered by exine projections and perine which cause it to be almost indistinguishable from the rest of the spore surface. The spores of the hybrid, *Bruchia* × *Trematodon* (Figs. 13–16), have distinct proximal and distal surfaces. The distal surface (Fig. 14) is covered with spinae-baculi which vary from pointed to blunt-tipped. The proximal surface is usually collapsed (Fig. 16). The aperture region of the proximal surface can be distinguished by the indistinct triangular annulus formed from verrucae or short spinae (Figs. 14–15). The first collar surrounding the annulus is typically covered with verrucae (Fig. 15) and is delimited by a row of short spinae which are often fused (Fig. 13). The second collar is also roughened with verrucae and may or may not be surrounded by a distinct ring of fused elements. Most of the hybrid spores, when viewed along the proximal surface, are collapsed, the proximal surface collapsing against the distal surface (Figs. 14, 16). When viewed on the distal surface the spores appear turgid (Figs. 14, 16), thus the percentage of collapsed spores could not be determined with any accuracy. Spores of the hybrid sporophyte and the putative parents were viewed under fluorescence microscopy to test for the presence of chlorophyll (see Paolillo & Kass, 1973). No chlorophyll fluorescence was observed in the thirty year old spores. Spores containing cytoplasm did



FIGURES 8–10. Scanning electron micrographs of rudimentary peristome on capsule of hybrid sporophyte.—8. View of mouth of urn with two complete teeth and fragments of others (×200).—9. Detailed view of dorsal surface of two teeth shown in Fig. 8 (×1000).—10. View of ventral surface of young peristome showing median line on each tooth. Deposition of material contributing to the unevenly thickened ventral surface of peristome ceases approximately four cells from base of each tooth and appears as a faint ridge (arrow) (×356).

TABLE 2. Summary of spore fluorescence analysis. Spore number represents counts from one collection of five capsules, three random fields of view (×25) per capsule for each taxon. Fluorescing spores indicate the presence of cytoplasm. Nonfluorescing spores lack cytoplasm.

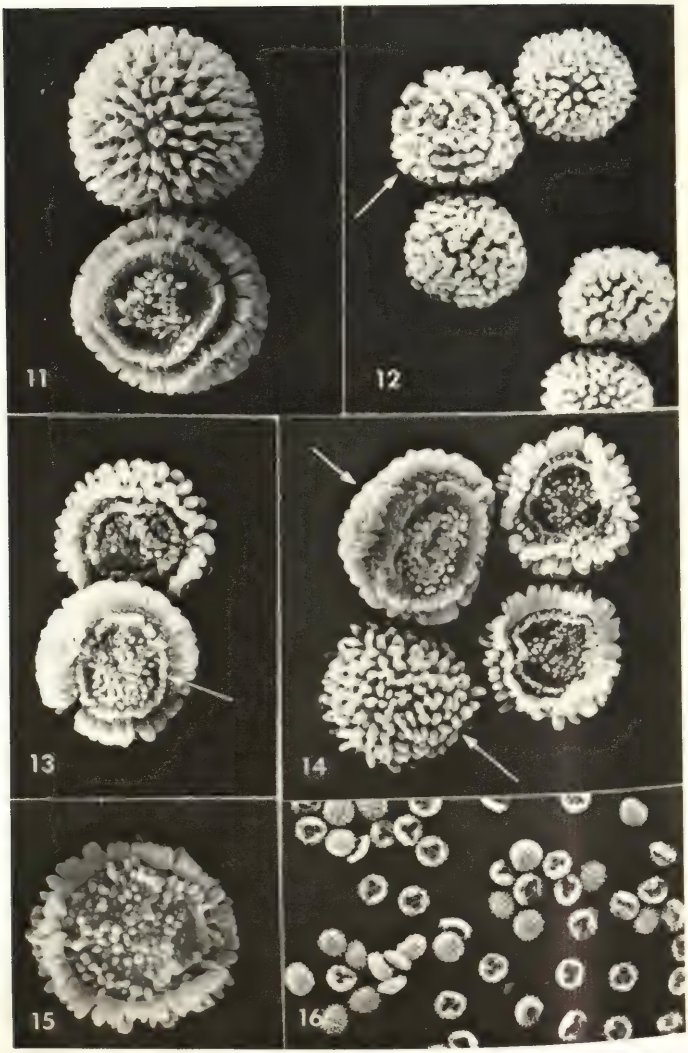
Taxon	Spore number	Fluorescent spores	Nonfluorescent spores	Percent fluorescence
Bruchia microspora	736	687	49	93.3%
Bruchia × *Trematodon*	994	69	925	6.9%
Trematodon longicollis	832	812	20	97.6%

fluoresce an intense yellow, however, whereas empty spores did not fluoresce. Utilizing this technique we determined that less than 7% of the spores of the hybrid sporophytes contained cytoplasm, whereas well over 90% of the spores of the putative parents contained cytoplasm. Results of the spore analyses are summarized in Table 2. The substances responsible for the cytoplasm fluorescence in the spores are unknown to us; however, Brown and Lemmon (1981) have recently shown that the interior of the spore of *Trematodon longicollis* is filled with storage lipids and the organelles are restricted to a thin peripheral layer. Thus, the fluorescence would appear to be associated with the lipid fraction of the cytoplasm.

Quantitative morphological features of both the gametophytes and the sporophytes of *Bruchia* and *Trematodon* were analyzed statistically using the Statistical Analysis System (SAS) package (Helwig & Council, 1979) for univariate statistics. The Numerical Taxonomy System of Multivariate Statistical Programs (NT-SYS) was used for cluster analysis and principal component analysis (PCA) (Rohlf et al., 1980). Techniques of cluster analysis and PCA were chosen because they require no *a priori* assignment of specimens to groups (Sneath & Sokal, 1973). For the cluster analysis, a distance matrix was generated from standardized character states and used in clustering the operational taxonomic units (OTUs) by the UPGMA (unweighted pair group method using arithmetic averages) option. The results of a cluster analysis are traditionally represented by a phenogram. For the PCA, the first three factors were extracted from a standardized character-by-character correlation matrix. Each factor is a composite of the effects of variances of all characters and is computed to maximize the distance between OTUs (Gilmartin, 1980). The standard procedure for representing the results of the PCA is by a three dimensional plot of the OTUs.

Analyses of gametophyte character measurements revealed that the gametophytes on which the hybrid sporophytes were attached were *Bruchia* gametophytes rather than *Trematodon* gametophytes. The statistical information presented here (Table 1; Figs. 17–18) includes only sporophyte characters. Analyses of sporophyte character states revealed three distinct groupings. The phenogram (Fig. 17) and the three-dimensional plot (Fig. 18) demonstrate that the hybrid sporophytes are distinctly different from the parental types but more closely resemble the *Bruchia* sporophyte. It should be noted, however, that these analyses are based only on quantitative characters (Table 1, first 11 characters). Qualitative characters, *i.e.* presence or absence of an annulus, presence or absence of a peristome, and spore morphology and viability are not included.

Discussion: Qualitative and quantitative studies of the sporophyte morphology of *Bruchia microspora* Nog. provide evidence supporting the hypothesis that two morphologically distinct sporophytes occur on the *Bruchia* gametophyte. The sporophyte with the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immersed, cleistocarpous capsule and turgid spores is the true *Bruchia microspora* sporophyte. The sporophyte with the exserted capsule, rudimentary annulus, fragmentary peristome and numerous collapsed spores is an F_1 intergeneric hybrid sporophyte resulting from a cross between *Bruchia microspora* and *Trematodon longicollis*. The formula and description of the hybrid follows:

Bruchia microspora Nog. ♀ × *Trematodon longicollis* Mx. ♂

Gametophyte that of *Bruchia microspora* Nog. Sporophyte with exserted capsules; seta yellowish to yellow-brown, 1.2–2.4 mm long × 0.16–0.22 mm wide; capsule erect, ovate to obovate, 1.59–1.90 mm long × 0.52–0.73 mm wide; neck well-developed, 0.42–0.70 mm long, stomata present, scattered; annulus region differentiated just below the rostrum but not dehiscing; rostrum erect, 0.29–0.44 mm long; rudimentary peristome of 16 short teeth, usually imperfectly developed and remaining within the "operculum"; spores variable, 22.8–26.5 μm in diameter, many collapsed and lacking cytoplasm; aperture region exhibiting an indistinct triangular annulus of verrucae or short spinae, outer collar surrounding annulus typically covered with verrucae, delimited by a row of short, frequently fused spinae, inner collar roughened with verrucae, occasionally surrounded by a distinct ring of fused elements, distal surface covered with pointed or blunt-tipped spinae-baculi; calyptra that of the female parent.

Specimens examined: (The following specimens are all from the island of Kyushu, Japan, Kumomoto Prefecture.) *Musci Japonici 354 K. Mayebara*, March, 1952 (B, BM, CINC, G, NY, S-PA, US); *K. Mayebara*, March 26, 1952 (B, BM, CINC, G, LAF, NY, S-PA, US); *Musci Japonici 565, K. Mayebara*, April 13, 1952 (B, BM, CINC, G, LAF, NY, S-PA, US); *K. Mayebara 678 p.p.*, May 2, 1936 (NICH) (holotype for *Bruchia microspora*); *K. Mayebara*, April 13, 1952 (NICH); *K. Mayebara*, March 23, 1952 (NICH).

The sporophyte and spores of *Bruchia microspora*, as described and illustrated in the protologue, exhibit a broad range of variability encompassing both the normal sporophyte and the hybrid sporophyte. In accordance with Recommendation 7B of the *Code* (Stafleu *et al.*, 1978) we have segregated that portion of the holotype consisting of non-hybrid sporophytes on *Bruchia* gametophytes as the lectotype. The sporophyte description for *Bruchia microspora* Nog. is emended as follows:

Sporophyte with capsule immersed; seta yellowish to yellow-brown, 0.65–1.04 mm long × 0.14–0.18 mm wide; capsules cleistocarpous, erect, ovate to obovate, 1.10–1.51 mm long × 0.49–0.60 mm wide; neck short 0.18–0.36 mm long, stomata present, scattered; rostrum erect, 1.10–1.51 mm long; spores 28.3–32 μm in diameter, turgid, exhibiting distinct proximal and distal surfaces, distal surface covered with spinae,

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FIGURES 11–16. Scanning electron micrographs of spores from selected specimens.—11. *Bruchia microspora* spores from proximal view (lower) and distal view (upper) (×1000).—12. *Trematodon longicollis* spores from proximal view (arrow) and distal views (×1000).—13. *Bruchia* × *Trematodon* spores showing proximal surfaces covered by short spinae. A ring of fused spinae (arrow) delimits the first collar (×1000).—14. *Bruchia* × *Trematodon* spores, three showing proximal surface and one showing distal surface. Spinae-baculi (arrows) vary from pointed to blunt tipped (×1000).—15. *Bruchia* × *Trematodon* spore showing proximal surface with indistinct annulus and collars covered by verrucae (×1600).—16. *Bruchia* × *Trematodon* spores showing collapsed proximal surfaces (×200).

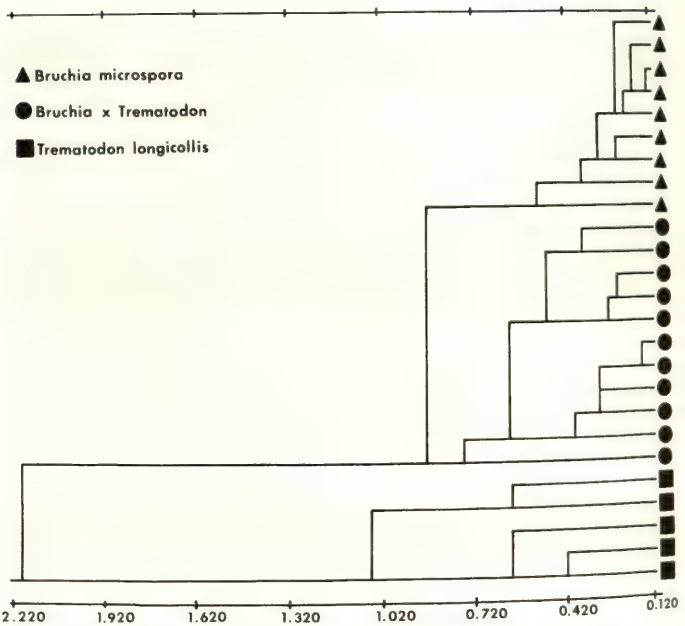

FIGURE 17. Phenogram of 25 OTUs (plants) resulting from UPGMA cluster analysis of the OTU × OTU distance matrix based on 11 sporophyte characters (cophenetic correlation coefficient, r = 0.957).

aperture surrounded by rows of spinae forming an annulus surrounded by two collars, outer collar smooth to sparsely verrucate, delimited by ring of spinae which are occasionally fused, inner collar usually smooth, delimited by a ring of fused spinae; calyptra mitrate.

Specimens examined: same as those cited under description of hybrid sporophyte.

Reports of naturally occurring hybrid sporophytes in mosses are scattered throughout the bryological literature (see summaries by Mönkemeyer, 1927; Wettstein, 1932; Anderson, 1980). The most convincing evidence for the occurrence of hybridization in mosses involves intergeneric crosses between weedy or semi-weedy taxa with similar gametophytes but in which the sporophyte of one parent is cleistocarpous, aperistomate and has a short seta, and that of the other parent is stegocarpous, peristomate and has a long seta (Anderson & Snider, 1982). The resulting hybrid sporophyte generally exhibits an intermediate morphology, influenced, in some instances, by the maternal parent. These include a seta of intermediate length, a rudimentary (usually non-functional) an-

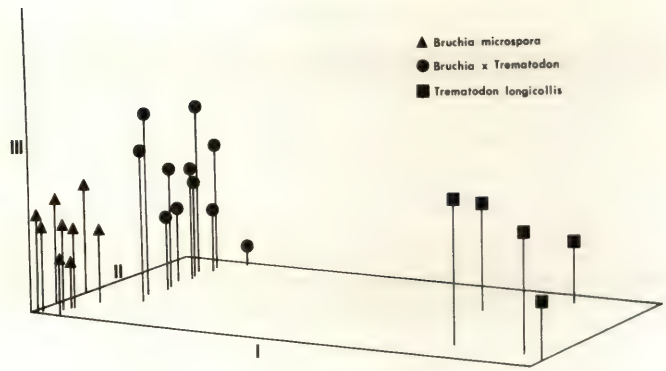

FIGURE 18. Principal component analysis. Projection of 25 OTUs (plants) onto the axes representing factors I, II and III based on the first 11 sporophyte characters from Table 1. The total variation explained by the model is 96.06% (factor I = 73.94%, II - 18.99%, III - 3.13%).

nulus, and a fragmentary peristome. Spores formed in the capsules of such sporophytes are usually shrunken and collapsed. Viable appearing, turgid spores occur with low frequency.

It is important to recognize that the origins of several of these natural hybrids have also been confirmed from cytological evidence. Anderson and Snider (unpublished) concluded that × *Pleuriditrichum marylandicum* (Andrews & Hermann, 1959) involved a population of *Pleuridium subulatum*, the chromosome number $n = 13$, crossed with a population of *Ditrichum pallidum*, the chromosome number $n = 26$. The putative reciprocal, *Ditrichum pallidum* × *Pleuridium subulatum* (Andrews, 1960) has been shown to actually involve a population of *D. pallidum*, the chromosome number $n =$ 26, crossed with a population of *P. subulatum*, the chromosome number $n = 26$ (Anderson & Snider, 1982). Anderson and Lemmon (1972) have demonstrated that hybrids reported between *Astomum ludovicianum* × *Weissia controversa* (Reese & Lemmon, 1965) involved populations of both taxa having the chromosome number $n = 13 + m$, whereas crosses between *Astomum muhlenbergianum* × *Weissia controversa* (Williams, 1966) involved populations having the chromosome number $n = 13$. The moss taxa for which intergeneric hybridization has been shown to occur generally occupy weedy habitats that have been recently disturbed and are sparsely vegetated—roadside embankments, pastures, woodland margins and utility company right-of-ways. Phenological development for each of the parents is the same or overlaps considerably, and gametangial production is high. Hybridization appears to occur only when colonies of the two parents are intermixed or are located within only a few millimeters of one another. The genera *Bruchia* and *Trematodon* both fulfill the criteria observed to favor hybridization in mosses.

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HETEROCLADIUM MACOUNII IN NORTH AMERICA[1]

W. B. SCHOFIELD[2]

In his revision of the North American species of *Heterocladium* B.S.G., Best (1901) described two new species: *H. macounii* Best and *H. heteropteroides* Best, the latter with a segregrated variety *filescens* Best. At the same time he commented that, although these taxa were confined to western North America, "forms analagous to *H. macounii* are found on the mountains of England, Scotland, Belgium, Germany and probably in the adjoining countries, and are usually referred to *H. heteropterum*." He noted also that *H. heteropteroides* "can be confidently looked for along the Atlantic coast, from Newfoundland northward. . . . "

A number of bryologists have misinterpreted Best's comments concerning European material. Dixon (1924), for example, treated *H. macounii* as a subspecies of *H. heteropterum* (Bruch) B. & S. and considered this taxon to be present in Great Britain. Allorge and Allorge (1952) made the same error, but they treated *H. macounii* as a variety of *H. heteropterum* when they reported it from the Azores (São Miguel). These authors stated that the specimens from the Azores showed on each leaf cell "2 papilles et un papille à chaque angle." They compared their material to specimens from Vancouver Island (Canada) and noted that the material from the Azores was identical in all critical characters. They made comparisons also with European specimens. Grout (1934) also concluded that *H. macounii* was "scarcely more than a variety of" *H. heteropteroides*.

Wallace (1956) accurately assessed the problem concerning European specimens: "It seems clear, then, that Best did not intend to imply that *H. macounii* occurs in Europe, but that there was there a plant bearing a relation to *H. heteropterum* similar to that which *H. macounii* bears to *H. heteropteroides*." He further stated that he considered *H. heteropteroides* and *H. macounii*, as represented in North America, to be essentially synonymous. The European material treated as "*H. macounii*" he would not consider to deserve "even varietal rank as distinct from *H. heteropterum*."

Heterocladium heteropteroides was noted by Billings and Anderson (1966) to be present in the gorges of the Southern Blue Ridge escarpment in the Appalachian Mountains of eastern United States, where it is "a common species." Anderson and Zander (1973) note the habitat as "on wet rocks, especially near waterfalls, and underneath overhanging ledges." They state the distribution as: "Alaska to Oregon and Idaho, North and South Carolina, Tennessee."

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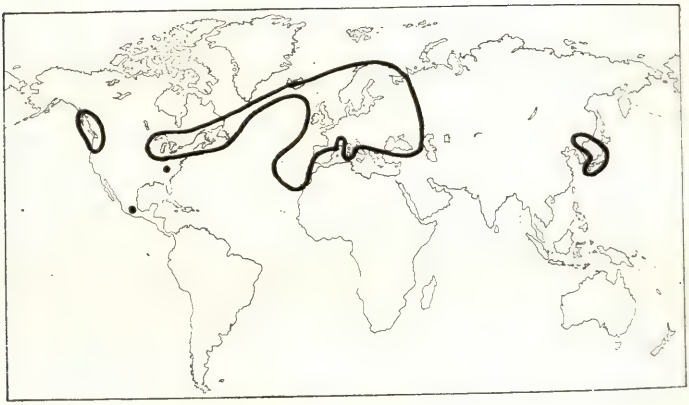

MAP 1. World distribution of the genus *Heterocladium* .

Lawton (1971) united *H. heteropteroides* and *H. macounii* and chose *H. macounii* as the name to represent the taxon, a clear application of Article 57.2 of the *International Code of Botanical Nomenclature*. The genus *Heterocladium*, as is apparent in *Index Muscorum*, has served as a reservoir for a diversity of taxa of very distant affinities. In the synonymy, species have been transferred to various genera in the Leskeaceae, Thuidiaceae, Fabroniaceae, Theliaceae, Entodontaceae, and Rigodiaceae. Indeed, *Heterocladium vancouveriense* (Kindb.) Kindb. in Macoun probably belongs to the Neckeraceae, where Lawton (1971) has placed it. Unfortunately it does not belong in the genus *Bestia* Broth., where Wijk and Margadant (1961) transferred it. Its accurate generic placement requires further study.

As currently constituted, *Heterocladium* consists of seven species: *H. angustifolium* (Dix.) Watanabe of Manchuria, its very close relative *H. gracillinum* Nog., of Japan, *H. tenellum* Deguchi & Suzuki of Japan, *H. heteropterum* (Brid.) B.S.G., predominantly of Europe, *H. procurrens* (Mitt.) Rau & Herv., and *H. macounii* Best of North America and the boreal *H. dimorphum* (Brid.) B. & S., widespread in Europe and North America. The single specimen determined as *H. dimorphum* from Ecuador (Mitten, 1869) remains doubtful.

Of these species, only four are represented by numerous collections. *Heterocladium dimorphum* and *H. procurrens* are relatively uniform in morphology, while *H. heteropterum* and *H. macounii* are represented by numerous morphotypes, which reflect their altered growth under varying conditions of moisture and illumination. Furthermore, *H. macounii* populations, in which sporophytes are not produced, show a progression of variant morphotypes as the clone becomes older and the gametophores become detached from a solid substratum. This detachment tends to result in an array of branching patterns, from highly regular to highly irregular. Accompanying these morphotype differences are changes in the stem leaves, and, to a degree, alterations in the orientation of the leaves.

TABLE 1: Number of *Heterocladium macounii* specimens examined.

Geographic Source of Specimens	Number of packets of specimens examined
British Columbia	320
Southeastern Alaska	43
California	7
Oregon	9
Washington	14
Tennessee	11
North Carolina	10
Mexico	3 (replicates of one collection)
Total	417

Degree of papillosity of leaf cells also varies considerably among the leaves of a single shoot and even on different cells of the same leaf.

These diverse morphotypes have been given formal names in *Heterocladium heteropterum*. *Index Muscorum* gives two subspecies and six varieties of which two are treated as forms in the synonymy. Fortunately, North American material, in spite of its parallel multiplicity of intergrading morphotypes, has not received an accompanying retinue of formally recognized infraspecific taxa.

In view of the extraordinary disjunctions of the eastern North American populations, the single Mexican population and the main range in western North America, it appeared appropriate to assess the distinctiveness of *Heterocladium heteropteriodes* Best from *H. macounii* Best. The conclusion reached is that they are identical. This analysis involved the examination of 417 herbarium specimens from UBC and TENN, supplemented by studies of the morphotype variability in living populations in both Eastern and Western North America.

The available information concerning *Heterocladium macounii* indicates that sporophytes are initiated in early summer. Rapid growth occurs in late summer, and meiosis occurs during the autumn. Opercula are shed in late winter to early spring, and spores are disseminated for several weeks. New sex organs appear on the gametophores with the initiation of vegetative growth in the spring.

Based on field observations, initial establishment of a gametophore is through the production of a stoloniferous system tightly affixed to the substratum. This irregularly branched shoot initiates innovations, and these initially are weakly and irregularly branched. These perennial innovations continue growth annually. In deeply shaded and humid sites the branches become isolated from the stolonifernus system as it decomposes and form an interwoven mat of elongate, usually irregularly branched shoots. In sites where the plants are exposed to direct illumination the plants tend to be more firmly affixed to the substratum, even when much of the stoloniferous system has disappeared. Branching by innovations is very dense, and the ultimate branching systems are slender, with relatively regular pinnate branches, and form a condensed turf-like mat. In these latter populations the branches curl downward toward the substratum when dry, while in the populations of deeply shaded sites the branches are not markedly altered in orientation upon desiccation.

In some western North American populations it is possible to find many different morphotypes within a single clone, with the more attenuate morphotypes appearing where

the shoots grow into less illuminated crannies or grottoes. In the eastern North American and Mexican specimens only these attenuated or flagelliform morphotypes are represented, and all populations appear to be confined to sites of high moisture and indirect illumination.

In the attenuate morphotypes, sex organs are usually absent. Indeed, no sex organs were noted in populations outside the Pacific coastal area of North America. Antheridium-bearing plants appear to be uncommon, and each gametophore bears very few perigonia. Within sporophyte-bearing populations, perigonial plants tend to be sparsely represented in spite of the fact that these same populations sometimes produce abundant sporophytes, especially on plants that occupy the sides and upper surfaces of boulders in mixed forest of alluvial sites.

The habitat diversity in western North American material is very wide, although most populations are found in areas of relatively low illumination and high humidity and are especially frequent in sites near water bodies. Rock types occupied are highly diverse, from calcareous sandstones and limestone to basalt, granite, quartzite, shale, and slate. Few trees appear to be a suitable substratum, but *Alnus rubra* Bong. (red alder), *Chamaecyparis nootkatensis* (Don) Spach (Alaska yellow cedar), *Thuja plicata* Don ex Don in Lamb (Western red cedar), and *Sequoia sempervirens* (Don) Endl. (redwood) sometimes possess colonies, which extend upward from the tree base and on the lower part of the trunk. When the trees fall, the moss will persist until the outer layers of the wood are soft from decomposition.

In western North America the bryophytic associates are numerous, especially in populations of better illuminated sites. Among the hepatic associates are the following, usually as scattered strands:

Anastrophyllum minutum (Schreb.) Schust.
Blepharostoma trichophyllum (L.) Dum.
Calypogeia fissa (L.) Raddi
Diplophyllum albicans (L.) Dum.
D. taxifolium (Wahlenb.) Dum.
Frullania tamarisci (L.) Dum. subsp. *nisquallensis* (Sull.) Hatt.
Lophocolea cuspidata (Nees) Limpr.
L. heterophylla (Schrad.) Dum.
Metzgeria conjugata Lindb.
M. leptoneura Spruce
Mylia taylorii (Hook.) S. Gray
Plagiochila porelloides (Torrey ex Nees) Lindenb.
P. satoi Hatt.
P. schofieldiana H. Inoue
Porella cordaeana (Hueb.) Moore
P. navicularis (Lehm. & Lindenb.) Lindb.
Radula auriculata Steph.
R. complanata (L.) Dum.
R. obtusiloba Steph. subsp. *polyclada* (Evans) Hatt.
Scapania americana K. Müll.
S. bolanderi Aust.

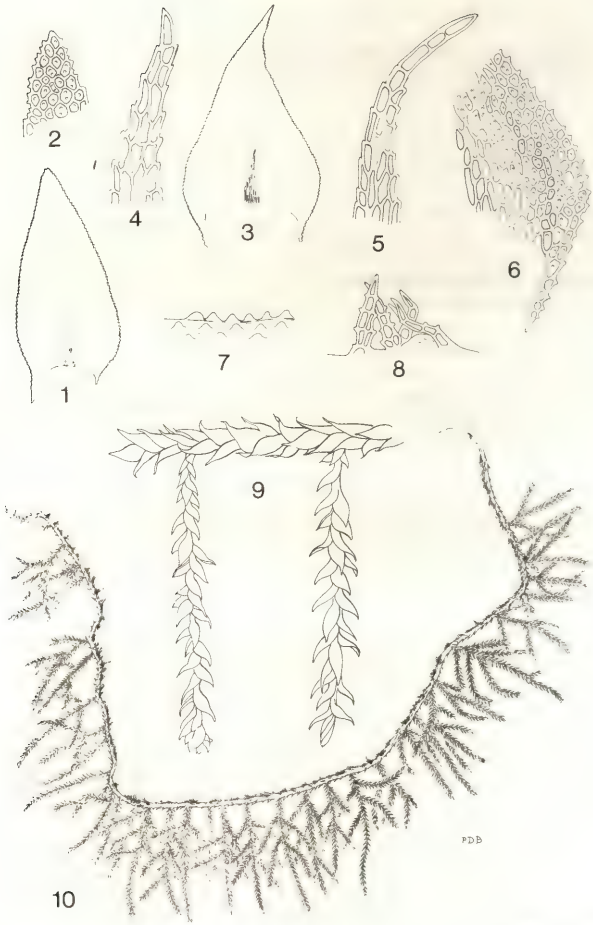

PLATE 1. *Heterocladium macounii*. Southern Appalachian populations.—Fig. 1. Leaf outline, leaf from flagelliform branch (× 85).—Fig. 2. Leaf apex, leaf from flagelliform branch (× 240).—Fig. 3. Leaf outline, leaf from stoloniferous shoot (× 85).—Figs. 4–5. Leaf apices, leaves from stoloniferous shoot × 240).—Fig. 6. Leaf base, showing decurrent and alar region (× 240).—Fig. 7. Stem papillae (× 240).—Fig. 8. Pseudoparaphyllia (× 240).—Fig. 9. Detail of flagelliform branches arising from stoloniferous shoot (× 12).—Fig. 10. Habit sketch of plant from underside of overhanging ledge (× 5).—(Figs. 9–10 drawn by Patricia Drukker-Brammall.)

Among the mosses associated with *H. macounii* in western North America are the following:

Barbula cylindrica (Tayl. ex Mackay) Schimp. ex Boul.
Brachythecium asperrimum (Mitt.) Sull.
Claopodium bolanderi Best.
C. crispifolium (Hook.) Ren. & Card.
C. whippleanum (Sull.) Ren. & Card.
Dicranum fuscescens Sm.
Heterocladium procurrens (Mitt.) Rau & Herv.
Hookeria lucens (Hedw.) Sm.
Hypnum dieckii Ren. & Card. ex Roell.
H. subimponens Lesq.
Isopterygium elegans (Brid.) Lindb.
Isothecium stoloniferum Brid.
Kindbergia oregana (Sull.) Ochrya
K. praelonga (Hedw.) Ochrya
Leucolepis menziesii (Hook.) Steere ex L. Koch
Mnium thomsonii Schimp.
Neckera douglasii Hook.
Plagiothecium denticulatum (Hedw.) B.S.G.
P. laetum B.S.G.
P. piliferum (Sw. ex C. J. Hartm.) B.S.G.
P. undulatum (Hedw.) B.S.G.
Pogonatum alpinum (Hedw.) Roehl var. *sylvaticum* (Brid.) Brid.
Porotrichum bigelovii (Sull.) Kindb.
Rhacomitrium occidentale Ren. & Card.
Rhizomnium glabrescens (Kindb.) T. Kop.
Thamnobryum neckeroides (Hook.) Lawt.
Trichostomun tenuirostre (Hook. & Tayl.) Lindg.

Associates of Southern Applachian specimens are rather fewer, and may reflect, in part, the smaller number of collections available. All specimens are from deeply shaded rock surfaces. Among the hepatics are *Jubula pennsylvanica* (Steph.) Evans., *Lophozia* sp., and *Metzgeria furcata* (L.) Dum., and among the mosses are *Anomodon attenuatus* (Hedw.) Hueb., *Fissidens cristatus* Wils. ex Mitt., *Isopterygium elegans* (Brid.) Lindb., and *Myurella sibirica* (C. Müll.) Reim.

The following description is based on material from throughout the range of the species, since, as clearly shown by Plates 1–3, there are no taxonomically significant differences in structure in populations found in any part of its range.

Primary stem creeping, sometimes stoloniform, 6–10 cm long, and tightly affixed to substratum by tufts of red smooth rhizoids, producing irregular innovations 1–4 cm long, these irregularly to sometimes very regularly pinnate-branched, the tertiary branches sometimes branched, especially when plants grow on diagonal to horizontal less shaded surfaces. In deep shade the main stems, and sometimes the branches, strongly flagelliform. In older long-established colonies the stems loosely affixed to the substratum and

PLATE 2. *Heterocladium macounii*, British Columbia populations.—Fig. 1. Habit sketch of attenuate morphotype with flagelliform branches, in wet condition, specimen inverted, scale as on plate.—Fig. 2. Detail of leaf arrangement in flagelliform branch in wet condition (× 10).—Fig. 3. Habit sketch of morphotype from more illuminated sites, in wet condition, scale as on plate.—Fig. 4. Habit of branch of Fig. 3 in dry condition (× 5).—Fig. 5. Leaf arrangement of main shoot of Fig. 3 (× 10).—(All figures drawn by Norman Eyolfson.)

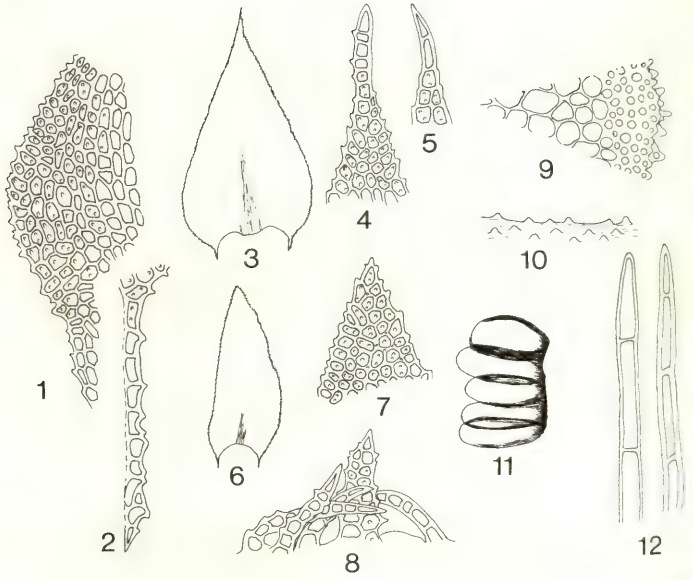

PLATE 3. *Heterocladium macounii*, British Columbia populations.—Fig. 1. Leaf base, main stem leaf, showing decurrent and alar region (× 240).—Fig. 2. Decurrent region of leaf (× 240).—Fig. 3. Leaf outline, leaf of main stem (× 80).—Fig. 4–5. Leaf apices, main stem leaves (× 240).—Fig. 6. Leaf outline, flagelliform branch (× 80).—Fig. 7. Apex from leaf of flagelliform branch (× 240).—Fig. 8. Pseudoparaphyllia × 240).—Fig. 9. Portion of cross-section of stem (× 240).—Fig. 10. Stem papillae (× 240).—Fig. 11. Annulus cells (× 240).—Fig. 12. Paraphyses: right from perigonium, left from perichaetium. (× 240).

rhizoids rare or absent, plants often forming their own substratum of decomposed gametophores.

Stems papillose, usually with scattered to abundant blunt to sharp papillae, occasionally with unicellular bulging outgrowths (paraphyllia?); pseudoparaphyllia scattered, filamentous or foliose, with both papillose and smooth cells. Stem cortex of 3–5 layers of stereid cells and 5–6 layers of larger inner cells; lacking a central strand.

Leaves of primary stoloniferous and larger shoots broadly triangular to cordate, usually with the base markedly cordate at least on one side, and decurrent down the stem, this decurrent area usually uniseriate, with the outer face, especially of the lowermost cell, sometimes forming a distinct tooth. These leaves 0.4–0.5 mm long and, at base, 0.3–0.4 mm wide, usually with an attenuate, sometimes twisted, apex ending in a single smooth cell. Costa broad at base, or sometimes weakly differentiated or absent, extending ½–⅔ up the leaf, usually forking irregularly near tip. Cells of leaf margin forming distinct small teeth. Leaf cells with variable number of papillae (1–5) that are over the exposed face, on the bounding walls between cells and sometimes projecting from cell angles. Median leaf cells elongate to rectangular 3(–4) × 20(–25) μm, often without papillae.

Cells toward margin generally more quadrate to isodiameteric, 4(–6) × 4(–6) μm, usually papillose. Apical cells often more elongate, terminating in a single pointed cell 10–15 μm long.

Leaves of main shoots that arise from stoloniferous system often secund to subsecund, costa more pronounced, and leaf apices sometimes more broadly acute, otherwise similar.

Leaves of flagelliform shoots and branches imbricate, smaller, 0.2–0.3 × 0.2–0.2 mm at base, ovate, with a broadly to narrowly acute apex; papillae often pronounced to apex; costa often broad at base and extending up ⅓ of leaf, occasionally unequally forked at tip, bases somewhat cordate and with uniseriate decurrent portion. Flagelliform branches somewhat brittle, possibly serving as vegetative propagants.

Dioicous, perigonia bulbiform, with broadly ovate non-papillose, ecostate leaves, leaf apices somewhat squarrose, lateral on main stem or larger lateral branches, 4–6 produced annually on each "fertile" branch. Antheridia 5–6 per perigonium, with admixed filiform paraphyses, composed of cells 54–56 × 15 μm rather thin walled (1–1.5 μm thick), apical cell with somewhat blunt tip.

Perichaetia bulbiform with narrowly ovate ecostate non-papillose leaves, innermost leaves narrowly ovate with an attenuate, markedly squarrose tip, lateral on main stem, 1–3 produced annually on each "fertile" branch. Archegonia 6–8 per perichaetium, with admixed filiform paraphyses composed of cells 40–80 × 12 μm and rather thick walled (3μm thick), apical cell pointed at tip.

Sporophyte with smooth red brown seta, lacking central strand; seta 0.6–1.5 cm. long, sporangium dark reddish-brown, not glossy when mature, horizontal to nodding, not or slightly curved, somewhat shrunken under mouth when dry, the urn 1–1.2 mm long; operculum rostate 0.5–1.2 mm long, the beak usually oblique and curved upward. Annulus of a single row of cells. Peristome double; exostomal teeth pale reddish brown through most of body, transparent at tips, with regular horizontal lines across the colored segments and papillae on the transparent apices. Endostomal teeth colorless, transparent, weakly papillose, cilia 2–3 between each tooth, one cilium usually shorter than other two. spores weakly papillose under light microscope, 9–10 μm. Exothecial cells longitudinally rectangular 60 × 30μm near base, smaller toward mouth, stomata phaneropore, confined to near base of sporangium 20–30 per sporangium or sometimes rare. Sporophyte-bearing material known from only western North America.

Distribution: Southwestern Alaska along the coast, southward to northern California, inland to the Columbia Mountains of British Columbia and Idaho, also in the Southern Blue Ridge Mountains in North Carolina, Tennessee, and South Carolina and from Puebla, Mexico. (See Map 2.)

Illustrations: Best (1901) Plate 14; Schofield (1969*a*) p. 145; Lawton (1971) Plate 144, figs. 8–13; Crum and Anderson (1981) Figure 428.

Chromosome Number: $n = 20$ (Ramsay & Schofield, 1980). Since in *H. procurrens* (Mitt.) Rau & Herv. $n = 10$, *H. macounii* is considered a polyploid. The count of each of these species is based on a single population.

The genus *Heterocladium* B.S.G. is a Northern Hemisphere genus, if the single collection from Ecuador is discounted. Based on the present distribution (see Map 1), the genus would appear to the Laurasian in origin. The only fossil records are from Europe (Dickson, 1973), from Pliocene sediments in Duab, U.S.S.R., and Frankfurt, Germany, and from Miocene sediments near Kracow, Poland. The Polish and Russian material are determined as *H. heteropterum*, while the German material is named only to genus.

Since no species possess any specialized vegetative diaspores, and since most species appear to be ecologically restricted, long distance dispersal seems unlikely to be of importance in dissemination. All species except *Heterocladium tenellum* are dioicous, and *H. tenellum*, in spite of its consistent sporophyte production, is extremely rare in Japan. *Heterocladium dimorphum* is an essentially Amphi-Atlantic species, with a wide distribution in both Europe and North America. This species may have originated before North America and the rest of the Laurasian landmass separated. *Heterocladium macounii* is clearly related to the predominantly European *H. heteropterum*. They differ in a number of features discussed later, occupy a similar spectrum of habitats, and show a comparable diversity of environmentally induced morphotypes. *Heterocladium procurrens* of western North America is sufficiently distinct from all other species in the genus that it has been placed in its own subgenus *Eurybrochis* Ren. & Card., which these authors separate on the basis of "loose, pellucid, smooth or scarcely papillose areolation" (Renauld & Cardot, 1890), compared to the more dense areolation and papillae on leaf cells of other species in the genus. The somewhat complanate leafy shoots with strongly divergent and squarrose leaves make the species the most distinctive in the genus.

The East Asiatic species, *H. angustiofolium* and *H. gracillimum*, appear to be closely related to each other and seem to be uncommon. Watanabe (1972) suggests that they may be related to *H. procurrens*. The other East Asian species, *H. tenellum*, of Japan, is the only monoicous species in the genus, and its relationships within the genus are unclear. Indeed, Deguchi and Suzuki (1974) suggest that it might be allied to *Pseudoleskeella papillosa* (Lindb.) Kindb. but they tentatively refer the species to *Heterocladium*.

The distribution of *H. macounii* is of particular interest, since it represents a disjunction between western North America and eastern North America. This kind of disjunction is well discussed by Wood (1970) for the vascular plants. In North America, as noted by Schofield (1969b), many bryophytes that are circumpolar in the Northern Hemisphere in their world distribution show the disjunction between eastern and western North America in their North American distribution. There are few species that are restricted to North America that show this disjunction; Schofield (1980) has noted only *Ditrichum ambiguum* Best, *Heterocladium macounii* Best, *Physcomitrium immersum* Sull., and *Hygrohypnum bestii* (Ren. & Bryhn ex Bryhn) Holz. ex Broth., the last of which is represented also in the Great Lakes area.

The following are representative bryophytes that show this east-west disjunction and are found in the Southern Appalachians. A number of other bryophytes shows the same basic disjunction, but they are taiga or tundra species or are sometimes found in the Northern Appalachians but not in the Southern Appalachians. Most of the species cited here show a wide distribution in western North America, especially near the coast in Alaska and British Columbia:

Hepatics:

Herbertus aduncus (Dicks.) S. Gray
Bazzania denudata (Torr. ex Gott.) Trev.
B. tricrenata (Wahlenb.) Lindb. in Broth.
B. trilobata (L.) S. Gray
Odontoschisma denudatum (Nees ex Mart.) Dum.
Mylia taylorii (Hook.) S. Gray

MAP 2. Distribution of *Heterocladium macounii* (based on herbarium specimens in UBC, TENN).

Nardia scalaris S. Gray
Sphenolobopsis pearsonii (Spruce) Schust.
Metzgeria leptoneura Spruce

Mosses:

Diphyscium foliosum (Hedw.) Mohr
Brachydontium trichodes (Web.) Milde
Campylopus atrovirens DeNot.
Dicranella rufescens (With.) Schimp.
Dicranodontium denudatum (Brid.) Britt. ex Williams
Anoectangium aestivum (Hedw.) Mitt.
Trichostomum tenuirostre (Hook. & Tayl.) Lindb.
Homalia trichomanoides (Hedw.) B.S.G.
Hookeria acutifolia Hook. & Grev.
Sematophyllum micans (Mitt.) Braithw.
Plagiothecium cavifolium (Brid.) Iwats.
Herzogiella striatella (Brid.) Iwats.
Isopterygiopsis muelleriana (Schimp.) Iwats.
Isopterygium elegans (Brid.) Lindb.
Hylocomium umbratum (Hedw.) B.S.G.

A number of these species commonly produce sporophytes in western North America and rarely or never in eastern North America, *e.g. Herbertus aduucus, Bazzania denudata*, and *Isopterygium elegans*, while others produce sporophytes in eastern North America but rarely, or never, in western North America, *e.g. Bazzania trilobata, Diphyscium foliosum*, and *Hylocomium umbratum*. Several are consistently vegetative in both parts of their North American range: *Sphenolobopsis pearsonii, Metzgeria leptoneura, Sematophyllum micans*. Several are extremely rare in both parts of their North American range: *Sphenolobopsis pearsonii, Brachydontium trichodes, Sematophyllum micans*.

This combination of features, although not consistent among all of the species, strongly suggests relictual fragments of a more continuous range of the past. Since a number of the species are confined in their total range to areas of cool temperatures and high precipitation, it seems probable that this continuous distribution was very ancient, possibly dating back to Tertiary times.

It is possible that the relictual populations of *Heterocladium macounii* are restricted to their very specialized habitat where they can not be supplanted by other plants. The mode of vegetative dissemination is presumably through accidental fragmentation or by extension from an original clone onto newly exposed substrata. In western North America the species seems to have considerably wider habitat tolerance. It is possible that this results from the greater genotypic diversity because it is sexually reproductive. Most of the western North American range of the species is in terrain that was ice-covered up to at least 10,000 years ago. This emphasizes the fact that most populations must have been derived from refugial populations south of the glacial boundary.

It is possible to suggest that the populations in the Southern Appalachians are the result of long-distance dispersed spores originating from west of the Rocky Mountains. In view

of the habitats of the species in both parts of its range, this seems unlikely. Sporophyte-bearing populations are generally within humid, usually forested sites. To get the spores air-borne, beyond the forest, then across North America and into its very specialized habitat requires an extraordinary multitude of fortuitous circumstances.

Although few specimens of *H. heteropterum* were examined in detail, the following features appear to distinguish it from *H. macounii*:

1. Leaves of main shoots conspicuously more divergent when dry.
2. Leafy shoots often somewhat compressed to subcomplanate.
3. Papillae often not apparent on leaves, or very small, usually one per cell.
4. Branching never as regular as is frequent in *H. macounii*.
5. Stems without papillae.

Although paraphyllia are noted in most European manuals, I found only pseudoparaphyllia; these are not as apparently papillose as those in *H. macounii* but are otherwise similar.

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BRYOLOGISTS I HAVE KNOWN

A. J. SHARP[1]

GEORGE E. NICHOLS

Although I had studied bryophytes in an amateurish way at Ohio Wesleyan University, Dr. Nichols was my first teacher who had had bryological training. His major interest was ecology, but he felt a biotic community could not be fully understood without including the mosses and hepatics. I registered in his beginning course in bryology in 1926 at the University of Michigan Biological Station, where Dr. Nichols (Chairman of the Botany Department, Yale University) taught during the summers. Later, during the summer of 1928, I took his course in advanced bryology.

He taught us many things in that beginning course: how to observe and recognize bryophytes in the field as well as the laboratory, how to do microscopic work without electricity, and how to be relatively comfortable while on extended field trips. He took us on three-day collecting excursions into the dune and bog area west of Mackinac City. Our manual was *The Bryophytes of Connecticut*, which he helped his major professor, Dr. A. W. Evans, prepare for the Connecticut Geological and Natural History Survey.

He was an exacting and challenging teacher; and at the end of eight weeks he asked us to recognize in the field, using only a handlens, 100 species of bryophytes. He could be pleasant or irritating as the occasion demanded. I was not the best student in the class, and he told me so. This stimulated me (as he knew it would) to return two years later to show him that I could be a better student. Fortunately he was convinced by my performance, for he asked me to go to Yale as a graduate student. I had been admitted to their graduate school for the spring (1933) session when one of the many bank failures of the time destroyed all my savings. Even though I never became one of his students at Yale, Dr. Nichols continued to give me professional advice and guidance until his death. Actually it was on his recommendation that I received my appointment to the botanical staff at the University of Tennessee. It was his encouragement that kept me interested in bryology even though other teachers and friends tried to divert me from it.

Dr. Nichols had an interesting family with which I became acquainted. Mrs. Nichols was not only fond of him, but also his students, and she rather "mothered" us and gave us friendly advice.

Dr. Nichols was rather humorously formal. In the field he always carried a bow tie on his belt, so that he could quickly put it on if we entered a restaurant, even in the "boondocks." He had an earthy sense of humor. One afternoon while walking from his

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FIGURE 1. George E. Nichols at Miner's Castle, Lake Superior, Michigan in 1937. Note tie on belt.

cabin to the laboratory, a gull "decorated" his Aladdin lantern. Entering our lab he said: "That dirty gull, with square miles of territory around her, had to pick on me."

A. J. GROUT

Dr. Grout and I first met at the New York A.A.A.S. meetings in December 1928. During the rather informal meetings of the Sullivant Moss Society, he and other members made the younger "neophytes" feel comfortable. He was well-known among the amateurs and "budding" bryologists, as well as the professionals, because of his manuals, *Mosses with a Handlens* (which included common hepatics) and *Mosses with a Handlens and Microscope*.

Soon thereafter he started a summer training course in bryology (particularly mosses) under the auspices of the Cold Spring Harbor Biological Laboratory, at his home near Newfane in the Green Mountains of Vermont. During the summer of 1934, Dr. Winona Welch and I studied in his small laboratory and adjacent fire-proof herbarium.

Dr. Grout was a typical New Englander, who had taught many years in the Brooklyn Boys High School in New York. On a ridge near his original home, he had built a summer cottage that had electricity, but the running water came from a cistern and was not used for drinking or in cooking. He was frugal, and rather than drill a well, water was carried

FIGURE 2. A. J. Grout and Mrs. Grout, Newfane, Vermont, 1932.

from a spring about one-quarter mile below the cabin. Two or three times a day, I donned a wooden yoke and carried two buckets of spring water up-slope for domestic use. For bathing the cistern water was heated by the sun, which meant that on cloudy days or in late evening baths were rather cool, but it represented typical New England thrift. It was from him that I got the habit of using government postal cards in much of my correspondence. The Grouts furnished me room and board for which I worked, in addition to hauling water, by filing mosses in his herbarium. He was aware of the great educational value of this service; I became acquainted with many new taxa. Another benefit gained was an ability to read Dr. Grout's script, which most people found impossible.

Dr. Grout had been a user of much calomel that loosened many of his teeth. Although not a complainer, this bothered him very much. Otherwise he was in fair health, and in his 70th year, spent two days climbing up and down Mt. LeConte in the Great Smoky Mountains National Park, collecting mosses along the trail.

He was critical up to a point: when he felt that a problem was demanding too much time or energy, his attitude was that we should let some future worker interested in extreme detail or nomenclatural legalism rectify the error, if one was made. He was tolerant of those with whom he did not agree, as is shown by the publication in his major three-volume work, *Moss Flora of North America*, of the contributions by others whose

FIGURE 3. Grout's summer cabin, Newfane, Vermont, 1932. Note solar water heater and rain gauge at left corner of porch.

points of view did not match his concepts. If he felt that he knew you well, in personal conversation or letter he could be rather abrupt.

Mrs. Grout was a quiet, kind person who frequently prevailed against his positive stance by gentle persuasion. She often softened his attitudes.

Dr. Grout received many letters requesting opinions and aid concerning bryological matters. Both his books and answering letters stimulated many workers to do additional studies of bryophytes.

EDWIN B. BARTRAM

Mr. Brartram, a Quaker who during middle life was an industrialist, on a visit with me indicated that he had made enough to support him and his wife for life and had retired early and decided to enjoy botanical studies. His first interest was vascular plants and ferns, but he soon became fascinated by the mosses of the southwestern United States and northern Latin America. He was very helpful to me in my early studies of Oklahoma mosses and continued to aid me, via correspondence, with the Southern Appalachian species.

Mr. Bartram was rather formal but pleasant, with a nice sense of humor. In a letter giving determinations of some collections I had sent to him, he wrote: "If that isn't *Merceya ligulata* I will eat my shirt buttons and all." (It was the first report of *Merceya* from eastern North America.)

Fortunately I was able to repay him in part by sending all my collections from Guatemala to him before the completion of his *Mosses of Guatemala*, for which he generously gave me more than ample credit.

FIGURE 4. Grout's laboratory, Newfane, Vermont (Dr. Winona H. Welch standing in the doorway). The concrete fireproof herbarium building is at left edge of photo, 1932.

ALEXANDER W. EVANS

Dr. Nichols introduced me to Dr. Evans from whom I soon solicited and received help in identifying Southern Appalachian liverworts. I found him a rather shy but pleasant tutor when I spent the summer of 1933 in the Osborn Botanical Library and Laboratory. During the first half of this century, he was the outstanding American hepaticologist; yet he was reticent in personal conversations, often enlivened by a calm sense of humor indicated by a quiet chuckle. Discussions with him and Dr. Hempstead Castle during that summer proved very useful to me.

He was extremely careful, and would politely call attention to errors. His knowledge extended beyond the liverworts. He noted a fragment of a strange moss in a collection of a liverwort I had sent to him for identification and sent it to R. S. Williams. The collection proved to be a first record for the genus in North America.

Later in life he turned his attention to lichens, about which by correspondence I learned much from him. Soon after he began studying lichens, several of us attending the Bryological Foray in the Keweenaw Peninsula of Michigan, sent a humorous telegram to him telling him to forget the lichens and return to full-time study of the hepatics. This backfired, and as far as I know, he never studied liverworts again. Yet he always seemed helpful and courteous to us thereafter, even presenting me with an almost complete set of his very useful reprints before his death.

A. LEROY ANDREWS

One would not expect a professor of Germanic languages, especially in ancient Icelandic, at Cornell University to be a leading bryologist. At times I felt that Dr. Andrews was more interested in bryology than languages. Although I met him several times, I learned more from his interesting letters and publications than from conversations. He had

FIGURE 5. A. J. Grout, A. W. Evans, and H. L. Blomquist, Currituck Point, North Carolina, spring 1937.

collected several rare species near Roan Mountain, Tennessee; and through our discussions of bryophyte distribution he initiated my interest in bryogeography.

Dr. Andrews was a careful worker. For example, Dr. Zennoske Iwatsuki and I in December 1957 collected a Pottiaceous moss on whose identity we could not agree. Dr. Iwatsuki called it *Molendoa sendtneriana*; and I foolishly said that it could not be that species, since it was not reported from North America. We sent it to five rather prominent American bryologists, no two of whom gave it even the same generic name. Dr. Andrews was the last to reply, and he agreed with Dr. Iwatsuki and sent along material from

Switzerland and Japan to prove his decision. He was excited by my collections to the point that shortly before his death, he urged me to spend the rest of my life doing nothing but exploring for plants, particularly bryophytes.

R. S. Williams

Elizabeth G. Britton, who worked in bryology at the New York Botanical Garden, recognized in the relatively untrained naturalist Mr. R. S. Williams potentialities for working with mosses. He was employed there to study and help care for these plants and served as my guide and mentor during my first research visit to that institution. Shy but kind, he easily held my attention by his accounts of his visits to Alaska (he participated in the Gold Rush), Latin America, and the Philippines. He invited me to his apartment, which was filled with collections of natural objects among which were many birds. He was an enthusiastic amateur ornithologist.

On one of my early visits to New York to discuss with him some bryological problems, I could not find him, although he was reported to be present. It was a cold December day, and I finally found him skating on a pond behind the Administration Building. At the time he was well over 70 years of age. Such outdoor activity was the only lure which diverted him from his study of mosses, to which he stubbornly devoted himself in later years.

He stimulated my further involvement with the mosses by congratulating me on the discovery of an exotic Homalioid moss which had been sent to him for study by Dr. Evans. I was embarrassed, for I had been trying to identify it as a hepatic species because of the small lobule of the leaf, characteristic of *Homaliadelphus*.

H. L. Blomquist

Soon after my arrival at the University of Tennessee, Dr. Blomquist and I became friends because of our common interest in Southern Appalachian liverworts and ferns. We sometimes met in Durham, North Carolina, or at the Highlands Biological Station in the Blue Ridge Mountains of North Carolina, but he stimulated me and taught me much in the exchange of ideas and collections by mail. One of his admonitions to me, in response to my protest about naming species after people, was that, in large genera such as *Plagiochila*, appropriate Latin adjectives for a taxon could no longer be found. He was informal and congenial, and during one of my early visits (1932) to Duke University he invited me to participate in a laboratory period of his bryology course, by which he taught me the importance of inviting outsiders to participate in my course and the usefulness of informal instruction.

Further information about some of the above byrologists is contained in the interesting discussion by Dr. W. C. Steere (1977).

Lewis E. Anderson

Among living bryologists, the one who has had the most influence (and still does) on me and my professional life was a graduate student whom I first met in Dr. Blomquist's

bryology laboratory in 1932. His name is Lewis E. Anderson, affectionately known as "Andy." For 50 years he has been my loyal friend, confidant, and sincere critic.

During the last half-century we have shared many things: field excursions, forays, classes, informal seminars in our homes; even students (Harold Robinson, Daniel Norris, Richard Zander) have had training with both of us. Recently we together completed a manuscript (Sharp & Anderson, 1981). We often exchanged lectures in our bryology courses, he, talking to my class about bryocytology, and I, to his class about bryogeography.

His graduate work was in cytology with Dr. Zirkle at the University of Pennsylvania, which provided him with the techniques and information which could be used with mosses. He soon became one of our leaders in the field of bryocytology. His findings, and those of his students, have greatly benefitted those of us with difficult problems in the taxonomy and distribution of mosses.

His family has been a great asset for him. His wife, Pat, has been a genial hostess for many bryologists and their students, even their foreign guests. Memories of the informal sessions in their pleasant home, interspersed with delightful music, are relished by many domestic and foreign scholars.

We have had many humorous episodes. Soon after the birth of their third child, I received a letter which stated that they were to have their *fourth* and *last* child. The fourth child proved to be twins, and the Andersons had five children, all of preschool age.

A rather non-descript moss in the Smoky Mountains was found several times by me in the 1950s, which I studied at intervals for a year or so. I finally gave up, and sent a packet of it to Andy to see if he knew it. He soon replied that it was *Hylocomium splendens* var. *tenue* described in The Bryologist by someone by the name of Sharp (it was later described as a new species of *Pterygynandrum* by Crum and Anderson). Felling "knee-high to a grasshopper" because of my stupidity, I grabbed a government postcard, and with the smallest quill-point pen available, under a low-power binocular microscope, I wrote "Thanks!" which I am sure he had difficulty finding and reading.

I welcomed the studies of Andy and his students on the bryophytes of the Southern Appalachians. These proved very useful, and stimulated us to get together with our classes at the Highland Biological Station and on field trips in the mountains, each of which was an enjoyable and educational experience.

I wish to take this opportunity to salute D. Lewis E. Anderson for his great contributions to American bryology culminating in the publication with the collaboration of Dr. Howard Crum of the *opus magnificum: Mosses of Eastern North America*. But most important I wish to thank him for the help he has given me, my students, and other bryologists during our fifty years of friendship.

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ON THE CONTINENTAL AFFILIATIONS OF THE MOSS FLORA OF HISPANIOLA[1,2]

WILLIAM CAMPBELL STEERE[3]

Abstract. Several large collections of mosses made in Hispaniola in recent years by bryologists very clearly demonstrate that approximately 100 species have a strong continental affinity and are known otherwise from the Southern Applachians, Mexico and Central America, and northern South America; they do not occur elsewhere in the West Indies. Phytogeographically speaking, it is as if a large chunk of Central America had broken off and drifted into the Caribbean Sea, carrying with it a continental flora. Many truly continental genera occur unexpectedly in Hispaniola, for example: *Amphidium, Anacolia, Andreaea, Anomodon, Aulacomnium, Bartramia, Bartramidula, Bryosedgwickia, Bryoxiphium, Ceratodon, Chrysoblastella, Dicranum, Diphyscium, Drepanocladus, Encalypta, Eurhynchium, Eustichia, Forsstroemia, Grimmia, Hedwigia, Hedwigidium, Herpetinerurum, Heterophyllium, Hylocomium, Leptodontium, Lepyrodon, Neckera, Oligotrichum, Orthodicranum, Palamocladium, Pleuridium, Pleurochaete, Pseudosymblepharis, Rhabdoweisia, Rhacocarpus, Racomitrium, Sciaromium, Schistidium* and *Zygodon*. Many of these genera are reported here for the first time from the West Indies.

In a comprehensive review of the moss flora of Haiti, based on three large collections of mosses made during the 1940's, Crum and Steere (1958) noted the "significant phytogeographic implications" inherent in the until then unrecognized occurrence in Hispaniola of many genera of mosses typically continental in their geographic distribution elsewhere. To quote: "The moss flora of the Antilles has generally been considered much more closely allied to that found in the sandstone and granitic mountains of [eastern] Venezuela, the Guianas and eastern Brazil than to the floras of the drier and mostly more calcareous uplands of continental America. Strong continental affiliations are shown by such genera as *Andreaea, Pleuridium, Orthodicranum, Pseudosymblepharis, Leptodontium, Pleurochaete, Grimmia, Sciaromium, Heterophyllium* and *Ptilium*. These genera include disjuncts from the ancient Appalachian Plateau of eastern United States, the Cordilleras of Mexico and Central America, and the Andes of South America. They are absent from other parts of the Antilles or, in a few instances, rare and local in Cuba and Jamaica, but not in Puerto Rico or the smaller West Indian islands."

As a result of much and extensive bryological collection carried out in the Dominican Republic in recent years, the list of Hispaniolan genera with strong continental affiliations given by Crum and Steere can now be much extended by the addition of such genera as *Anacolia, Anomodon, Aulacomnium, Bartramia, Bartramidula, Bryosedgwickia, Bryoxiphium, Ceratodon, Chrysoblastella, Dicranum, Diphyscium, Drepanocladus, En-*

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[1]On the occasion of his retirement, this paper is dedicated to Professor Lewis E. Anderson, who has spent so many years studying the moss flora of the Southern Appalachians, and who will find so many Appalachian species familiar to him in the appended list.

[2]All specimens cited here that were collected in Hispaniola by W. R. Buck, W. D. Reese, and W. C. Steere are the result of field work supported by National Science Foundation grant DEB-8021729 to the New York Botanical Garden.

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calypta, Eurhynchium, Forsstroemia, Hedwigia, Hedwigidium, Herpetineurum, Hylocomium, Lepyrodon, Neckera, Oligotrichum, Palamocladium, Rhabdoweisia, Rhacocarpus, Racomitrium, Rigodium, Schistidium, and *Zygodon.*

That the moss flora of Hispaniola contains a very large proportion (over 90 taxa) of continental species which, with few exceptions, do not occur elsewhere in the West Indies, but only on the mainland of North, Central and South America, is a clear-cut fact well illustrated by the accompanying list. To explain this curious and fascinating bryogeographical disjunction is another matter, however. On the basis of both zoogeographical data and geological observations, Schuchert (1935) postulated that the Greater Antilles, in various combinations, had been connected by land to Central America, in the region which is now Honduras and Nicaragua, not only once but several times. After summing up his biogeographical evidence, Schuchert said (1935: 109), "If the latter students [*i.e.* geologists and stratigraphers] know anything at all, it is that the present Greater Antilles are not oceanic or volcanic islands, but consist of continental rocks and are now fragments of a once greater Central America; that this fragmentation began, in one place or another, shortly after the mountain making in the late Cretaceous; and that the Greater Antilles were completely severed from the continent off and on; that the separation became permanent probably in Miocene, and certainly in Pliocene, time; and finally, that the present island geography was initiated in the Pliocene and completed in the Pleistocene." Unfortunately for all the easy answers which Schuchert's conclusions make possible for phytogeographers, more recent geologists and biogeographers do not accept them. For example, in a review of the paleogeography and geological history of the Greater Antilles, Khudoley and Meyerhoff (1971) consider the Greater Antilles as of volcanic origin and not truly continental. In a relatively recent treatise on zoogeography, Darlington (1965) recognizes no historical land connections at all and states that the fauna of the Greater Antilles consists only of those stocks of animals which are in some manner able to traverse salt water. He concludes (p. 516), "The simple explanation of all this is that terrestrial vertebrates have reached the Greater Antilles across salt water; that the existing and late-fossil forms are an original accumulation, mostly distributed along original routes of immigration; and that most of the significant Greater Antillean groups have come from Central America by way of Cuba or (less often) Jamaica at a time when the Central American fauna was a mixture of both North and South American elements." In a discussion of the vegetation of the Antilles, Howard (1973) mentions in several different contexts the floristic affinities and disjunctions between genera of vascular plants of the Greater Antilles and Central America. Also, he says (p. 34), "Genera with a geographic range reaching the United States occur in the southern peninsula, and the central range of mountains [of Hispaniola]. The same pattern exists for genera of Hispaniola which also occur in the Lesser Antilles, in Central America or in South America."

The extensive collections from the Dominican Republic (and a few collections from Haiti) which provide the material for this paper represent the work of many collectors since the 1940's. The collector who was active over the longest period of time, from 1946 until his death in 1982, was José de Js. Jiménez, a medical doctor from Santiago de los Caballeros. Several of his earliest collections, identified by E. B. Bartram, served as the basis for an often overlooked report (Jiménez, 1954). Another earlier collector, H. A. Allard of the U.S. Department of Agriculture, made a large and representative collection

of bryophytes between October 1947 and January 1948, mostly in the province of La Vega and near the city of Santo Domingo. Allard's specimens are in the National Herbarium (US), with duplicates at the University of Michigan (MICH) and the New York Botanical Garden (NY). In December 1964, G. C. Jones and the bryologist, D. H. Norris, collected in the Dominican Republic and, for a longer time in 1967, D. H. Norris, G. J. Gastony, and G. C. Jones visited many localities throughout the republic. Between 1968 and 1977, Alain Liogier made occasional collections of bryophytes while carrying on a general survey of the vascular flora. In 1976, W. S. Judd made a small but critical collection of bryophytes, of which many were new to the Dominican Republic (Judd, 1980). Between August 1979 and February 1980, G. L. Smith, while collecting mostly vascular plants, was able to accumulate a large collection of bryophytes. Since 1980, Thomas Zanoni (with several associates) has continued to collect bryophytes in spite of his fuller commitment to the higher plants. In 1981 two bryologists, W. R. Buck and W. D. Reese, made excellent and substantial collections of bryophytes in the Dominican Republic during the months of March and April, as did W. R. Buck and W. C. Steere in April and May, 1982. The author has identified all the collections (with the exception of those submitted to specialists, which are duly noted in the following list) made by Allard, Buck, Liogier, Reese, Smith, and Zanoni, and either the original specimens or duplicates are at NY. The author has also reviewed the earlier collections made by Jiménez and has identified those collected in recent years; duplicates of all are at NY. Moreover, through the generosity of the collectors, many duplicates of the collections made by Judd and by Norris and his associates are at NY.

Now that so many large new collections of mosses from the Dominican Republic have become available for study, the time seems highly appropriate for a review of the disjunct continental elements in the moss flora of the whole island of Hispaniola, with special reference to those taxa most typical of 1) the Southern Appalachians, 2) Central America, and 3) South America, especially the northern Andes. Buck and Steere (1983) have very recently published a check-list of the mosses of Haiti and the Dominican Republic.

A List of otherwise Continental Mosses that occur in Hispaniola

Amblystegium varium (Hedw.) Lindb. DOMINICAN REPUBLIC: Prov. Pedernales, Río Mulito, *Buck 4471*.—This widespread continental species was previously reported from Hispaniola, from Haiti, by Crum and Steere (1958). It is very widely distributed in the United States and Canada, and extends southward to Mexico, Guatemala, and Panama. In the West Indies, however, it is known only from Hispaniola.

Anacolia laevisphaera (Tayl.) Flow. DOMINICAN REPUBLIC: Prov. La Vega, near summit, Alto de la Bandera, *Buck 5431 c.fr., 5456 c.fr., Reese 15862, Smith 10336* (det. D. Griffin, III).—Originally described from Ecuador, this species is now known to occur in the southwestern United States, in Mexico and Central America, and it is widespread in the Andes of South America. This is the first report of the genus from the West Indies.

Andreaea rupestris Hedw. DOMINICAN REPUBLIC: Prov. La Vega, near summit, Pico Duarte, alt. 3175 m, *Norris, Gastony & Jones 5834*; vicinity of La Lagunita, alt. 2850 m, *Norris, Gastony & Jones 5400, 5484, 5509*; Valle Nuevo-San José de Ocoa road near

Pyramid, *Norris, Gastony & Jones 7380* (all det. Norris).—A very widely distributed moss of mountainous areas, almost always growing on acidic rocks. This continental moss was first reported from the Dominican Republic (and the West Indies) by Thériot (1944; as *A. petrophila* Ehrh.): Prov. Azua, top of La Pelona, alt. 3100 m (*Ekman 13650*).

Anoectangium incurvans (Schimp.) Bartr. DOMINICAN REPUBLIC: Prov. Pedernales, Aceitillar, Sierra de Baoruco, *Judd 1601* (det. Judd); 37 km north of Cabo Rojo, *Buck 4426*.—Originally described from Mexico and reported from Guatemala by Bartram (1949), this species is new to the West Indies; filed at NY is a collection from Venezuela (leg. J. Steyermark et al.; det. H. Robinson).

Aptychella proligera (Broth.) Herz. [*A. americana* (Card.) Broth.]. DOMINICAN REPUBLIC: Prov. Peravia, La Nevera, alt. 6800–6900 ft., *Buck 5280, Reese 15705, 15715, 15730* (all det. Buck).—This species is known elsewhere from the Andes of Bolivia and Colombia, and from Brazil (Robinson, 1967); it has been reported from the West Indies previously from Cuba (Bizot, 1965) and from Jamaica (Crum & Bartram, 1958).

Aulacomnium palustre (Hedw.) Schwaegr. DOMINICAN REPUBLIC: Prov. La Vega, between Constanza and La Nuez, *Jones & Norris 1316–6*; Valle Nuevo-San José de Ocoa road near Pyramid, *Norris, Gastony & Jones 7258, 7262* (all det. Norris); *Reese 15757; Steere 23135*.—This is an extremely common and almost cosmopolitan species in North America north of Mexico; known from Venezuela, Ecuador, Bolivia, Peru, Paraguay and Brazil. It was reported earlier from the Dominican Republic by Crum and Anderson (1981), but without giving either the locality or the name of a collector.

Barbula bescherellei Sauerb. in Jaeg. DOMINICAN REPUBLIC: Prov. La Vega, Alto de la Bandera, *Buck 5450, 5451, 5454, Reese 15861, 15899*; La Culata, *Reese 15834*. Prov. La Estrelleta, north of Angel Feliz, *Buck 4589*. Prov. Peravia, La Nuez, *Buck 5214, 5217, 5226, Reese 15677*. Prov. Pedernales, near El Aguacate, *Buck 4721, Reese 15298, 15300*. HAITI: Dépt. Sud'est, Mare Rouge, *Adams & Zanoni 11304, 11310*. Dépt. l'Ouest, opposite Aniceto Martínez, *Buck 4805*.—As noted by Crum and Steere (1958), *Barbula subteretiuscula* Card. and several other species have been described in the difficult complex of *B. bescherellei* and *B. acuta* (Brid.) Brid. However, so many collections have now become available for study, with so many intermediate forms, that it seems best to call them all *B. bescherellei*, a species of the southwestern United States, Mexico, and Central America.

Barbella pendula (Sull.) Fleisch. DOMINICAN REPUBLIC: Prov. Santiago, Pico Diego de Ocampo, alt. 1170 m, *Judd 1530, 1552* (both det. Judd). Prov. Pedernales, Las Abejas, *Buck 4269*.—Previously reported from the Dominican Republic by Judd (1980) and by Crum and Anderson (1981). Elsewhere, this species occurs in the United States in Florida, Louisiana, and Mississippi, extending to eastern Mexico; also present in Japan and China and perhaps elsewhere in Asia (cf. Reese, 1966).

Barbula fidelis Crum & Steere. DOMINICAN REPUBLIC: Prov. Pedernales, Las Abejas, *Buck 4287, Reese 15008*; south of El Aguacate, *Buck 4752*.—This species was originally described from Haiti (Crum & Steere, 1958), from a collection made on the Morne des Commissaires (*Mackaness 72*), and the collections from Prov. de Pedernales agree well with it; it is most closely related to *B. convoluta*, a wholly continental species.

Barbula inaequalifolia Tayl. DOMINICAN REPUBLIC: Prov. La Vega, near summit, Alto do la Bandera, alt. 2800 m, *Smith 10334b* (det. R. H. Zander), *Reese 15893*.—HAITI: roadside between Furcy and Kenskoff, *F. P. Mackaness 134*.—First described from the

Andes of Ecuador, this typically continental species is now known from Peru, Colombia, and Mexico, as well as from the United States, from North Carolina; it has not been reported previously from the Antilles.

Barbula laevigata (Mitt.) Jaeg. [*Didymodon* Zander]. DOMINICAN REPUBLIC: Prov. Peravia, La Nuez, *Buck 5222* (det. Zander, as *Didymodon*).—An Andean species first described from Ecuador, and now known from Colombia to Bolivia, this moss is one of several which have a disjunct distribution pattern between the Andes and Hispaniola.

Barbula pringlei Card. DOMINICAN REPUBLIC: Prov. La Vega, between La Nuez and Pyramid, *Judd 1298, 1299* (det. Zander).—Judd (1980) reported these two collections as new to Hispaniola and the West Indies; the species was previously known from Mexico and Central America.

Bartramia angustifolia Mitt. DOMINICAN REPUBLIC: Prov. La Vega, vicinity of La Lagunita, alt. 2800 m, *Norris, Gastony & Jones 5618* (det. Norris).—An Andean species which is new to the West Indies, as is also the genus.

Bartramia postosica Mont. DOMINICAN REPUBLIC: Prov. La Vega, between Constanza and La Nuez, alt. 5000–8000 ft., *Jones & Norris 1331B* (det. Norris).—In South America this species ranges from Chile to Colombia in the Andes, thence to Central America and Mexico; this is apparently the first collection from the Antilles.

Bartramidula tuerckheimii (C. Müll.) Par. DOMINICAN REPUBLIC: Prov. La Vega, between Constanza and La Nuez, alt. 5000–8000 ft., *Jones & Norris 1324A*; vicinity of La Lagunita, alt. 2800 m, *Norris, Gastony & Jones 5544* (both det. Norris).—This is a remarkable range extension and disjunction for a species which was previously endemic to Guatemala (Bartram, 1949).

Brachymenium bulbiferum Bartr. DOMINICAN REPUBLIC: Prov. Barahona, Monteada Nueva, near Polo, alt. 3300 ft., *Judd 1602* (det. Judd).—Judd (1980) was the first to report this species from Hispaniola and the West Indies, from the specimen cited here; it is known elsewhere only in Costa Rica, the type locality.

Brotherella tenuirostris (Bruch & Schimp. ex Sull.) Fleisch. [*Hypnum holdridgei* Crum & Steere]. The type (and only) specimen of *H. holdridgei* Crum & Steere was collected in Haiti, on the top of Morne de la Selle at an altitude of 2575 m (*Holdridge 1890a*), in minor admixture with *Dicranum flagellare* Hedw. (Crum & Steere, 1958). On an annotation slip accompanying the isotype specimen of *H. holdridgei* at NY, H. Ando has written, "closely related to *Brotherella tenuirostris*." A careful reexamination of the type material has led me to agree fully with Ando, an eminent specialist on the Hypnaceae and related groups, and to realize that it is not only "closely related to" but identical with *B. tenuirostris*. The alar and other basal leaf cells are a clear golden yellow in color, a characteristic far more typical of the Sematophyllaceae than the Hypnaceae, and they match very well the illustration provided by Crum and Anderson (1981). In the same place, Crum and Anderson characterize this species as "Appalachian-Ozarkian" in its geographical distribution, although its range extends considerably north of that area, reaching southern Canada and even Newfoundland. It should now be searched for in the Dominican Republic.

Bryoerythrophyllum recurvirostre (Hedw.) Chen. DOMINICAN REPUBLIC: Prov. La Vega, Valle Nuevo-San José de Ocoa road, Pyramid site, *Reese 15788*; Alto do la Bandera, *Reese 15878*.—Although widespread in North America from Alaska through Mexico to Central America, and almost throughout the United States and Canada, this

essentially continental species seems to have been reported previously from the West Indies only from Puerto Rico (Crum & Steere, 1957).

Bryosedgwickia densa (Hook.) Biz. & P.-Varde HAITI: Dépt. Sud'est, near Seguin, *Adams & Zanoni 11268, 11288* (both det. Buck).—Known previously from Central and South America, this genus provides an interesting addition to the West Indian bryoflora.

Bryoxiphium norvegicum (Brid.) Mitt. DOMINICAN REPUBLIC: Prov. La Vega, Valle Neuvo-San José de Ocoa road, near Pyramid, *Norris, Gastony & Jones 7325* (det. Norris).—This handsome species was originally described from a specimen from Iceland, where it is abundant. It is now known to be widely distributed in North America, in rather specialized habitats. Its somewhat erratic distribution pattern has been discussed by Steere (1937) and by Löve and Löve (1953). A typically continental species, this was first reported from the Dominican Republic by Crum and Anderson (1981), although without identification of either locality or collector.

Calyptothecium turgescens Broth. & Thér. DOMINICAN REPUBLIC: Prov. La Vega, between Constanza & Buena Vista, alt. 2000–4000 ft., *Jones & Norris 1232* (det. Norris); south bank of Río Los Guanos, alt. 1100–1200 m, *Norris, Gastony & Jones 4984, 5125* (both det. Norris). Until now, this continental species has been known only from Central America, from Costa Rica and Guatemala.

Calyptrochaeta haitensis (Crum & Steere) Crosby (*Eriopus* Crum & Steere), described from the Morne des Commissaires, Haiti (Crum & Steere, 1958), was the first member of a genus well represented in the Andes of South America to be discovered in the West Indies; it has also been collected in and reported from Costa Rica by Crosby (1974). More recently, it has been reported from Mexico by Delgadillo M. and Juárez G. (1982).

Campylium stellatum (Hedw.) C. Jens. DOMINICAN REPUBLIC: Prov. Pedernales, near El Aguacate, *Buck 4722*; Las Abejas, *Zanoni & Mejía 16646*. HAITI: Dépt. Sud'est, Mare Rouge, alt. 1900 m, *Adams & Zanoni 11298, 11302, 11305, 11314, 11315, 11317*.—A continental species, this moss is widespread in northern North America but extends much farther south in the mountains. In the West, it extends from Arctic Alaska to Mexico and Guatemala, but it does not seem to have been reported previously from the Antilles.

Ceratodon purpureus (Hedw.) Brid. DOMINICAN REPUBLIC: Prov. La Vega, Constanza-La Nuez road, alt. 5000–8000 ft., *Jones & Norris 1091* (det. Norris).—This common weedy species is widely distributed and abundant in the Americas, extending from Alaska south through Mexico and Central America to Colombia; it was reported earlier from Haiti by Crum and Steere (1958).

Ceratodon stenocarpus B.S.G. DOMINICAN REPUBLIC: Prov. La Vega, Constanza-La Nuez road, alt. 5000–8000 ft., *Jones & Norris 1080*; Valle Nuevo-San José de Ocoa road, alt. 2500 m, *Norris, Gastony & Jones 7134, 7315* (all det. Norris); Constanza, alt. 1600 m, *Liogier 22220*; Valle Nuevo military post, *Zanoni 16452*; Pyramid site, *Buck 5308, Reese 15771a, 15774, 15785*; Alto de la Bandera, *Buck 5430, 5433, Reese 15866, 15882*. Prov. Independencia, near crest of Sierra de Beiba, *Norris, Gastony & Jones 6370* (det. Norris). Prov. San Juan, north of Río Arriba del Norte, alto. 6500 ft., *R. A. & E. S. Howard 9050*. Prov. Peravia, La Nevera, *Buck 5327*. Prov. San Cristóbal, Mano Matuey, *Buck 5156*.—In North America, this relatively common species occurs in the southwestern United States and extends through Mexico to Central America; in South America, it ranges southward in the Andes to Bolivia. Surprisingly enough, it seems to be new for the West Indies.

Chrysoblastella chilensis (Mont.) Reim. DOMINICAN REPUBLIC: Prov. La Vega, Constanza-Valle Nuevo road, alt. 2300 m, *Norris, Gastony & Jones 7083*; vicinity of La Lagunita, alt. 2800–2900 m, *Norris, Gastony & Jones 5515* (all det. Norris).—In South America, this Andean species ranges from Ecuador through Peru and Bolivia to Chile, thence to the subantarctic to Marion Island and South Georgia; it is an amazing discovery for the West Indies (cf. Buck, 1981).

Dicranella vaginata (Hook.) Mitt. [*Anisothecium* Mitt.]. DOMINICAN REPUBLIC: Prov. La Vega, Valle Nuevo, alt. 2300 m, *Jiménez M-70*.—This typically continental species occurs at high altitudes in Mexico, Costa Rica and South America, but does not seem to have been collected previously in the West Indies.

Dicranum flagellare Hedw. [*Orthodicranum* Loeske]. DOMINICAN REPUBLIC: Prov. La Vega, vincinity of Constanza, *Allard 17618, 17688i*; near La Ciénaga, alt. 1200–1800 m, *Norris, Gastony & Jones 5394, 5397* (det. Norris); vicinity of La Lagunita, alt. 2800–2900 m, *Norris, Gastony & Jones 5487, 5660, 5676* (all det. Norris); Pyramids site, *Reese 15757*; Alto de la Bandera, *Buck 5418*. Prov. Peravia, La Nevera, *Reese 15754, Steere 22714*; alt. 850 m, *Liogier 26005*.—Crum and Steere (1958) reported three specimens from higher altitudes in Haiti, the first records for the West Indies. Elsewhere, this is a species of continental affiliation which is widely distributed through southeastern Canada and the eastern United States; it extends southward through Mexico to Guatemala and Panama.

Dicranum rhabdocarpum Sull. [*Orthodicranum* Loeske]. DOMINICAN REPUBLIC: Prov. La Vega, Constanza-La Nuez road, alt. 5000–8000 ft., *Jones & Norris 1317A, 1085, 1086A* (all det. Norris).—This strongly continental species was originally described from Colorado, and is now known southward in the Rocky Mountains to Arizona and New Mexico, thence through Mexico to Guatemala; it is a phytogeographically interesting addition to the flora of Hispaniola and the West Indies.

Dicranum sumichrastii Duby. DOMINICAN REPUBLIC: Prov. Pedernales, Sierra de Baoruco, alt. 2000 m, *Smith 10198* (det. Griffin).—Originally described from Mexico, this species is now known also from Central America, which gives its occurrence in Hispaniola a special phytogeographical significance.

Diphyscium domingense (Brid.) Buck & Steere [Moscosoa 2(1): 34. 1983]. Prov. La Vega, Alto de la Bandera, alt. 2800 m, *Buck 5432, Reese 15890*.—This species, first described in 1827, is almost certainly conspecific with taxa described much later from Mexico and Central America, so that a careful comparison and study would be well worth while. This species may be distinguished from *D. foliosum* (Hedw.) Mohr, which has been reported from Jamaica by Crum and Bartram (1958) and from Cuba by Bizot (1965), by the smooth-awned perichaetial leaves.

Encalypta ciliata Hedw. DOMINICAN REPUBLIC: Prov. La Vega, Alto de la Bandera, alt. 2800 m, *Buck 5455* (det. D. G. Horton), *5456, Reese 15853, 15870*.—In North America, this species is very widely distributed from Alaska to Mexico, although it does not seem to reach the easternmost United States; in South America it occurs in Ecuador. This typically continental species is reported here for the first time from the West Indies.

Encalypta flowersiana Horton.—This recently described species (Horton, 1979) illustrates the point of this paper in the very simplest terms, as it is known from only three localities, from the type locality in Haiti (Dépt. l'Ouest, near summit of Pic la Selle, alt. ca. 2675 m, *Wetmore 3129*, type) and from Guatemala (Dept. Huehuetenango, region of

Chemal, Sierra de los Cuchumatanes, alt. ca. 3300 m, *Standley 83090*). More recently, Horton (1983) reported it from Texas. The Haitian specimen was reported earlier by Crum (1965) as *E. vulgaris* Hedw., which was the first record of the genus *Encalypta* in the West Indies.

Entodon serrulatus Mitt. [*E. stenocarpus* (Besch.) Jaeg.] HAITI: Vicinity of Furcy, Morne de Wejan, alt. 1300 m, *E. C. Leonard 4620a* (det. Buck).—This otherwise Mexican and Central American (Guatemala) species is new to the flora of Hispaniola and the West Indies.

Erpodium glaziovii Hampe. DOMINICAN REPUBLIC: Prov. Santiago, Santiago de los Caballeros, alt. 600 ft., *Judd 1308*.—Judd (1980) was the first to report this South American species from the West Indies; it is known elsewhere only from Brazil and Paraguay.

Eurhynchium praelongum (Hedw.) B.S.G. DOMINICAN REPUBLIC: Prov. Pedernales, vicinity of El Aguacate, *Reese 15299*.—A continental species which is very widely distributed in North America, especially in the western mountains, from Alaska to California, and farther south to Mexico, Guatemala and Costa Rica; rare in the eastern United States. It does not seem to have been reported previously from the Antilles.

Eurhynchium pulchellum (Hedw.) Jenn. DOMINICAN REPUBLIC: Prov. La Vega, Alto de la Bandera, *Buck 5443*. Prov. Peravia, La Nevera, *Buck 5235, 5281, Reese 15683*.—A very common and abundant species of eastern and northern North America which has apparently not been reported previously from the West Indies, although it occurs from Mexico through Central America to northern South America.

Eustichia longirostris (Brid.) Brid.—This strongly continental species was reported from the Dominican Republic by Thériot [1944; as *E. spruceana* (C. Müll.) Par.] from Loma Sucia, San José de Ocoa, alt. 2300 m (*Ekman 12006*; duplicate at NY). Elsewhere, it is known from Mexico, Guatemala, Costa Rica and South America, where it extends southward to Chile and Argentina.

Fissidens steerei Grout. DOMINICAN REPUBLIC: Prov. Pedernales, Mencia-Aguas Negras Road, *Buck 4481*.—Originally described by Grout from material collected in Mexico (Yucatán) and Guatemala, this continental species is now known (fide Pursell, 1979) from other states of Mexico, Honduras, Panama and Venezuela; Pursell (1979) reported it also from Puerto Rico.

Forsstroemia trichomitria (Hedw.) Lindb. DOMINICAN REPUBLIC: Prov. La Vega, near Constanza, alt. 1400 m, *Norris, Gastony & Jones 7074A* (det. Norris).—In North America, this species is widespread in the eastern part, becoming more common southward; it reaches northeastern Mexico, but does not seem to have been collected earlier in the Antilles.

Grimmia affinis Hornsch. DOMINICAN REPUBLIC: Prov. La Vega, Pico Duarte, alt. 3170 m, *Liogier 25032* (det. Judd, FLAS, NY; Steere, NY); near summit, Alto de la Bandera, alt. 2800 m, *Buck 5463* (det. E. Lawton), *Reese 15863, 15874, 15886, Smith 10337*; Pyramids site, *Zanoni 16463*.—This typically continental species is widely distributed in North America, especially in the northern part, but extends farther south in the eastern and western mountains; southward through Mexico, Guatemala, and Costa Rica to the Andes of South America. Moreover, it also has a wide world distribution, but does not seem to have been reported previously from the West Indies. Thériot (1944) described *Grimmia antillarum* Thér. as a new species from the Dominican Republic, from

Prov. Azua, Los Vallecitos de Yaque, alt. 2500 m (*Ekman 13650*). He compared *G. antillarum* with both *G. commutata* Huebn. [= *G. ovalis* (Hedw.) Lindb.] and *G. campestris* Burch. and distinguished it from them by the longer capsule and by calyptra differences. However, the capsule length of the type specimen of *G. antillarum* (isotype at NY) falls well within the range of variation of the capsules of *G. affinis*. The bistratose leaf margins and leaf lamina are also quite typical of *G. affinis*; in fact, Thériot's illustrations compare well in morphology (if not in quality) with those of Crum and Anderson (1981), Flowers (1973) and Lawton (1975: plate 56). In addition to morphological considerations, to me an overwhelming argument for considering *Grimmia antillarum* as a synonym of *G. affinis*, a truly continental species, is the large number of such continental species reported in this paper, none of which needs to be described as new.

Grimmia laevigata (Brid.) Brid. DOMINICAN REPUBLIC: Prov. la Vega, near summit, Alto de la Bandera, alt. 2800 m, *Reese 15847*.—This continental species is very widespread in the United States and southern Canada; it also reaches northern Mexico, but has not been reported from the West Indies before now.

Hedwigia ciliata (Hedw.) P.-Beauv. DOMINICAN REPUBLIC: Prov. La Vega, Valle Nuevo, alt. 2280 m, *Jiménez M-69, M-75*; Arroyo de la Compartición, La Rucilla, alt. 2600 m, *Liogier 25046* (det. Judd, FLAS, NY; Steere, NY); Constanza-La Nuez road, alt. 5000–8000 ft., *Jones & Norris 1083B* (det. Norris); Valle Nuevo-San José de Ocoa road, alt. 2500 m, *Norris, Gastony & Jones 7352* (det. Norris); near summit, Alto de la Bandera, alt. 2800 m, *Reese 15869, 15880, Smith 10319*; Valle Nuevo military post, *Zanoni 12352*; Pyramid site, *Zanoni 16457*.—Thériot reported this species from the Dominican Republic (1944; as *H. albicans* fo. *stricta*), from Pico de Valle Nuevo, alt. 2600 m (*Ekman 13775*). This nearly cosmopolitan continental species is very widespread almost throughout North America where acidic rocks occur, also in Mexico and Central America and northern South America. Crum and Anderson (1981) include Santo Domingo in the geographic range given for this species, undoubtedly based on Thériot's report.

Hedwigidium integrifolium (P.-Beauv.) Dixon [*H. imberbe* (Smith) B.S.G.]. DOMINICAN REPUBLIC: Prov. La Vega, Valle Nuevo, alt. 2680 m, *Jiménez M-78*; Constanza-La Nuez road, 5000–8000 ft., *Jones & Norris 1288B, 1083B, 1330C*; Mt. Casabito, El Río-Jayaco road, *Norris, Gastony & Jones 7080*; Valle Nuevo-San José de Ocoa road, alt. 2500 m, *Norris, Gastony & Jones 7344, 7353, 7381, 7606*; summit of Pico Duarte, alt. 3175 m, *Norris, Gastony & Jones 5842; Liogier 28033*; vicinity of La Lagunita, alt. 2800–2900 m, *Norris, Gastony & Jones 5391, 5395, 5406, 5438, 5488, 5495, 5646, 5677, 5680* (all det. Norris); near summit, Alto de la Bandera, alt. 2800 m, *Buck 5457, 5469, Reese 15787, 15884, 15892, Smith 10319a, 10323, 10337a*; Pyramids site, *Reese 15787*.—This typically continental species occurs at high altitudes in Mexico and Central America and in the Andes of South America; it has not been reported previously from the West Indies.

Herpetineurum toccoae (Sull. & Lesq.) Card. DOMINICAN REPUBLIC: Prov. Azua, Cañada Miguel Martín, alt. 1500 m, *Mejía & Zanoni 8267*.—Bartram (in Jiménez, 1954) first reported this species as new to the Dominican Republic and the Antilles, based on three specimens collected by Jiménez on rocks in the Río Igua (*M-8, M-32, M-39*). This clear-cut and easily recognized species was originally described from Toccoa Falls, Georgia, but is now known from several states in the Southeast, extending west to

Oklahoma and Texas, and southward to Mexico and Guatemala. It has been reported elsewhere from widely scattered stations in Asia, Indonesia, Oceania, and Africa.

Heterophyllium affine (Hook. ex Kunth) Fleisch.—This continental species was reported from Haiti by Thériot (1944), from Croix-des-Bouquets, Badeau, alt. 1300–2000 m (*Ekman 7696*). Later, Crum and Bartram (1958) reported it from Jamaica, from below New Haven Gap, alt. 1500–1600 ft. (*Maxon & Killip 966*). Elsewhere in North America, this species occurs in the Southern Appalachians, with southerly extensions to Mexico, Guatemala, and Colombia.

Holomitrium flexuosum Mitt. DOMINICAN REPUBLIC: Prov. La Vega, Constanza-La Nuez road, alt. 5000–8000 ft., *Jones & Norris 1079* (det. Norris).—This characteristically continental species is known elsewhere in Mexico, Guatemala, Costa Rica, and Ecuador; not previously reported from Hispaniola or the West Indies (cf. Hegewald, 1978).

Hylocomium dentatum (Thér.) Steere, comb. nov. (*Pterobryopsis dentata* Thér., Trav. Bryol. 2: 18. 1944; *Hylocomium giganteum* Bartram, Bryologist 49: 124. 1946).—Thériot (1944) described his new species from the Dominican Republic, *Pterobryopsis dentata*, from "Cordillera Central, prov. de La Vega, Constanza, Loma La Vieja, top of Mountains, mossy forest, 2.075 m." (*Ekman 14032*). An isotype specimen at NY bears the further information, "on the ground," which is obviously not the correct habitat for a species of *Pterobryopsis*. This moss is spectacularly large and frondose, but not at all in the same manner as *Pterobryopsis*, in which the plants are dendroid. Neither is it at all related to *Meteorium*, to which Arzeni (1954) assigned it, probably because of the occasionally plicate or longitudinally undulate stem leaves. It is incomprehensible to me how both authors could have overlooked the abundant paraphyllia. To be sure, the paraphyllia are somewhat appressed to the stem, but they become perfectly obvious when the leaves have been dissected away from the stem. Like the Guatemalan collections cited by Bartram, the Ekman collection from the Dominican Republic is sterile. I am grateful to Donald Pfister (FH) and to John Engel (F) for the loan of the Guatemalan collections (*Standley 60947*, type; *62714*) upon which Bartram based his new species, *Hylocomium giganteum*, which is identical with *Pterobryopsis dentata* Thér. Of *H. giganteum*, Bartram (1946, 1949) said most appropriately, "This magnificent moss is a striking addition to the tropical American flora," a statement which is equally true today. It is also an outstanding example of the disjunction of continental taxa between Central America and Hispaniola.

Hypnum amabile (Mitt.) Hampe. DOMINICAN REPUBLIC: Prov. La Vega, Valle Nuevo-San José de Ocoa road, alt. 2500 m, *Norris, Gastony & Jones 7094, 7195* (both det. Norris); Valle Nuevo military post, *Zanoni 12356*.—Previously known from Mexico, Central America, and the Andes of northern South America, this species seems to be new to the West Indies.

Leptodontium excelsum (Sull.) E.G. Britt. DOMINICAN REPUBLIC: Prov. La Vega, waterfall near Constanza, alt. 4000 ft., *Jones & Norris 1273*; Constanza-La Nuez road, alt. 5000–8000 ft., *Jones & Norris 1076D*; 3 km west of La Ciénaga, *Norris, Gastony & Jones 5393*; Valle Nuevo-San José de Ocoa road, alt. 2500 m, *Norris, Gastony & Jones 7599* (all det. Norris).—This species occurs at rather high altitudes (±6000 ft.) in the Southern Appalchians in Virginia, Tennessee, Georgia, and North Carolina, where it was first discovered. Although Crum (1965) reported this continental species from Haiti, Crum and Anderson (1981) now hold the opinion that tropical American specimens bearing this name may well be reduced forms of *L. ulocalyx* (C. Müll.) Mitt.

Leptodontium luteum (Tayl.) Mitt. DOMINICAN REPUBLIC: Prov. La Vega, Valle Nuevo-San José de Ocoa road, alt. 2500 m, *Norris, Gastony & Jones 7104, 7153, 7193* (all det. Norris); Pyramids site, *Buck 5312*.—First described from Ecuador, this Andean species is also known from Columbia, Peru, and Bolivia; Zander (1972) cites a collection from Tanganyika. This seems to be the first report from the West Indies.

Leptodontium sulfureum (C. Müll.) Mitt. DOMINICAN REPUBLIC: Prov. La Vega, El Montazo, alt. 1900 m, *Jiménez M-57* (det. Bartram).—This typically continental species extends from Mexico through Central America and southward in the Andes of South America to Bolivia; it is new to the West Indies.

Leptodontium ulocalyx (C. Müll.) Mitt. DOMINICAN REPUBLIC: Prov. La Vega, near Valle Nuevo, alt. 2560 m, *Allard 17529, Jiménez M-76* (det. Bartram), *Judd 1268*; Valle Nuevo-La Nuez road, alt. 2040 m, *Judd 1303*; Alto de la Bandera, *Buck 5428, Reese 15854, Zanoni 12359*. Prov. Peravia, La Nevera, *Buck 5261, 5287, Liogier 21584, 24949, Mejía & Zanoni 8706, 8723, 8741, Reese 15692, 15699, 15694, 15728, Smith 10340, Zanoni & Mejía 12221, 12238, 12241, Zanoni et al. 12213*. Prov. Pedernales, Sierra de Baoruco, near height of land, alt. 2000 m, *Smith 10197*; Alto del Toro, alt. 2000 m, *Liogier 26988*.—Judd (1980) has reported his two collections cited above, as *L. viticulosoides* (P.-Beauv.) Wijk & Marg. var. *panamense* (Lor.) Zander. This species, which extends from Mexico through Central America to northern South America, has also been reported from high altitudes in Haiti by Thériot [1944; as *L. subcirrifolium* (C. Müll.) Par.] and by Crum and Steere (1958).

Lepyrodon tomentosus (Hook.) Mitt. DOMINICAN REPUBLIC: Prov. La Vega, Valle Nuevo-La Nuez Road, alt. 2100 m, *Judd 1242, 1252* (both det. Judd); Alto de la Bandera, alt. 2800 m, *Reese 15851*.—This species occurs in the mountains of Central America and in the Andes of South America from Colombia to Chile. Thériot (1944) reported this otherwise continental species from the Dominican Republic, with the remark "espèce nouvelle pour les Antilles"; it was also reported by Judd (1980), on the basis of his own collections cited above.

Leucodon julaceus (Hedw.) Sull. DOMINICAN REPUBLIC: Prov. La Vega, waterfall west of Constanza, alt. 4000 ft., *Jones & Norris 1255* (det. Norris).—This continental species is widely distributed in eastern North America, from southern Canada to Florida and Texas, and reaches northeastern Mexico. However, this seems to be the first collection known from Hispaniola and the West Indies.

Meiothecium tenerum Mitt. HAITI: Dépt. Sud'est, near Seguin, road to Mare Rouge, *Adams & Zanoni 11270a* (det. Buck).—This species was also reported from two localities in the Morne des Comissaires by Crum and Steere (1958). Known elsewhere from continental localities in Mexico, British Honduras, Costa Rica, Bolivia, Argentina, and Brazil (type locality). Crum and Anderson (1981) include this species in their *Mosses of Eastern North America* on the basis of a single specimen collected near St. Augustine, Florida, in 1877 by J. Donnell Smith, which was described by Austin as *Fabronia donnellii*.

Neckera urnigera C. Müll. DOMINICAN REPUBLIC: Prov. La Vega, Río los Guanos, alt. 1100–1200 m, *Norris, Gastony & Jones 5205A*. Prov. Independencia, alt. 1200 m, *Norris, Gastony & Jones 6750* (both det. Norris); alt. 1550 m, *Smith 10235c*. Prov. La Estrelleta, north of Angel Feliz, *Buck 4544, 4600*.—Previously known from Mexico, Guatemala and Panama, this species is new to the West Indies, as is also the genus.

Oligotrichum aligerum Mitt. DOMINICAN REPUBLIC: Prov. La Vega, vicinity of La Lagunita, alt. 2800 m, *Norris, Gastony & Jones 5606* (det. Norris). Prov. Peravia, La Nevera, *Buck 5242, Reese 15681, 15703*.—This species has a remarkable distribution, as it extends from Alaska southward to Oregon, jumps to Mexico and Costa Rica; also in Japan. It was reported from Jamaica by Bartram (1936) and Crum and Bartram (1958). Its occurrence in Jamaica makes this report from Hispaniola seem less improbable.

Orthotrichum anomalum Hedw.—This continental species was reported from a single locality in Haiti by Crum and Steere (1958), but it has not yet been collected in the Dominican Republic. It is widespread in Canada and the northern United States and extends south in the eastern and western mountains to North Carolina, Arizona, northern Mexico, and Guatemala.

Palamocladium leskeoides (Hook.) E. G. Britt. [*Pleuropus bonplandii* (Hook.) Broth.; *P. leskeoides* (Hook.) Steere]. DOMINICAN REPUBLIC: Prov. La Vega, El Montazo, alt. 1900 m, *Jiménez M-58*; vicinity of Constanza, *Allard 17575, 17597p*; Loma Campana, *Allard 18701*; Constanza-Valle Nuevo Road, alt. 1615 m, *Judd 1285* (det. Judd), alt. 2015 m, *Smith 10314*. Prov. Azua, Cañada Miguel Martín, 1500–1600 m, *Mejía & Zanoni 8268, 8276*. Prov. Pedernales, near Oviedo, *Buck 4447, Reese 15012*; Las Abejas, *Buck 4336, 4363, Reese 14919, 15009, Zanoni & Mejía 16707*; near El Aguacate, *Buck 4734, 4736, Reese 15263, 15264, 15280*. Prov. La Estrelleta, north of Angel Feliz, *Buck 4555, 4608, Reese 15154*. Prov. San Rafael, along Haitian border, alt. 1400 m, *Norris, Gastony & Jones 6473* (det. Norris). Prov. Independencia, near crest of Sierra de Neiba, alt. 1700–2000 m, *Norris, Gastony & Jones 6373* (det. Norris); south of El Aguacate, *Buck 4694, Reese 15235*. Prov. Puerto Plata, Pico El Murazo, *Buck 4960, Reese 15466, 15489*. HAITI: Dépt. Sud'est, Mare Rouge-Sequin road, alt. 5900 ft., *Adams & Zanoni 11320*.—Also, this species was reported from several other localities in Haiti by Crum and Steere (1958), and from the Dominican Republic by Judd (1980; as *Homaliothecium leskeoides* (Hook.) Robinson), from the specimen cited above. Crum and Bartram (1958) pointed out that, in spite of several reports of the occurrence of this species in the West Indies, most were based on misidentifications. The abundant material cited here, including 12 collections from Haiti, removes all doubts concerning the presence of this handsome species in the West Indies. Elsewhere, it occurs in the southern United States and extends from Mexico to northern South America. Crum and Anderson (1981) include Cuba and Jamaica in its range.

Papillaria penicillata (Dozy & Molk.) Broth. DOMINICAN REPUBLIC: Prov. La Vega, Valle Nuevo, alt. 2430 m, *Jiménez M-72*; vicinity of Constanza, *Allard* (22 numbers!); bank of Río Los Guanos, alt. 1100–1200 m, *Norris, Gastony & Jones 5893* (det. Norris). Prov. San Rafael, Sierra de Neiba, along Haitian border, *Norris, Gastony & Jones 6887, 6898* (both det. Norris). Prov. Independencia, crest of Sierra de Neiba along Haitian border, *Norris, Gastony & Jones 5972, 6161, 6376, 6391* (all det. Norris). Prov. La Estrelleta, north of Angel Feliz, *Buck 4795, Reese 15320, 15325*. Prov. Pedernales, Las Abejas, *Buck 4274, 4340, 4371, Reese 14909, 14935, 14937, 14966, Steere 22927, 22956, Zanoni & Mejía 16680*; near El Aguacate, *Buck 4727, Reese 15287*; north of Los Arroyos, *Steere 22903*. HAITI: Dépt. Sud'est, at Savane Lage near Mare Rouge, *Adams & Zanoni 11322, 11325*.—Crum and Steere (1958) reported several other collections from Haiti. In the West Indies, this somewhat enigmatic species is also known from Jamaica

(Crum & Bartram, 1958); elsewhere it is strictly continental, in Panama, Ecuador, Venezuela, Colombia, Peru, and Brazil.

Phyllodrepanium falcifolium (Schwaegr.) Crosby. [*Drepanophyllum* Wijk & Marg.; *D. fulvum* Hook.]. In his original description of *Fissidens falcifolius* (Sp. Musc. Suppl. 1(2): 9. 1816), Schwaegrichen said, "In insula Borboniae et Hispaniola lectum dedere Richard et Thuillier, arboris innatum." Florschütz (1964) reviewed the specimen from Hispaniola, but said of it only "(examined Thuillier s.n., Domingo, G)." It apparently has not been collected in either Haiti or the Dominican Republic since the original collection was made, and I have seen no material at all from Hispaniola except for the type (courtesy of Patricia Geissler, G). As a consequence, I share the doubts expressed by Crosby (1970) concerning the accuracy of the label in the Schwaegrichen herbarium; it has been known for some time that the specimen purportedly from Bourbon Island [La Réunion] actually came from British Guiana! This strongly continental species is represented by NY by collections from British and French Guiana, Suriname, Venezuela, Colombia, Ecuador, and Brazil; to these countries Crosby (1970) has added Trinidad, Honduras, and Panama.

Pilosium chlorophyllum (Hornsch.) Par. DOMINICAN REPUBLIC: Prov. La Vega, vicinity of Piedra Blanca, *Allard* (nearly 50 numbers!); Loma Compana, *Allard 18682, 18813*; Río Yuna, Rancho Arriba, *Liogier 26042*. Prov. Trujillo, Valdesia Valley, *Allard 16614*.—Williams (1930) described *Pilosium serrulatum* R. S. Williams from Haiti, from Département du Nord, St. Michel de l'Atalaye (*E. C. Leonard 7248*). In the type collection, as well shown in Williams's illustration (1930), the leaf apex is distinctly serrulate. In his review of the North American species of *Pilosium*, Grout (1945) included *P. serrulatum* with some reservation; he said, "Doubtfully more than a variety of *P. chlorophyllum*, with more distinctly serrulate leaves, narrower median cells and more numerous enlarged basal cells." In my opinion, *P. serrulatum* is only a geographical race or form that does not merit formal taxonomic recognition, but should be placed in the synonymy of *P. chlorophyllum*. In an examination of 20 specimens from Central and South America picked at random, I found that many of them show some tendency toward the production of serrulate leaf apices. On the other hand, none of the many Allard collections has leaves as serrulate as in the type of *P. serrulatum*, and most of them were quite entire. Outside of Hispaniola, this species is common and widely distributed throughout Central America and South America as far south as Brazil and Bolivia; I have seen no specimens from elsewhere in the West Indies.

Pilotrichella cuspidans Ren. & Card. [*Renauldia subpilifera* R. S. Williams]. DOMINICAN REPUBLIC: Prov. La Vega, vicinity of Constanza, *Allard 17620*; Constanza-Valle Nuevo road, alt. 1525 m, *Norris, Gastony & Jones 7481*; bank of Río los Guanos, *Norris & Jones 4887, 4999* (both det. Norris). Prov. Independencia, near crest of Sierra de Neiba along Haitian border, *Norris, Gastony & Jones 5954, 6206* (all det. Norris); 4 km south of El Aguacate, *Buck 4701, Reese 15229, 15233, 15236*. Prov. La Estrelleta, Sierra de Neiba, *Buck 4573, Reese 15150, 15340*. Prov. Barahona, Monteada Nueva, *Steere 22825*. Prov. Pedernales, Las Abejas, *Buck 4295, 4343, 4401, Reese 14898, 14935, 14988, Steere 22838, 22912, 22943*; near El Aguacate, *Reese 15267, 15280, 15290*; north of Los Arroyos, *Steere 22901*. Prov. Peravia, La Nevera, *Reese 15705*. Prov. Puerto Plata, Pico El Murazo, *Buck 4916*. HAITI: Bois Coutre, near Morne de la Selle (*C. R. Orcutt s.n.*; syntype of *P. pungens* Bartram in herb.; NY). Between Kenskoff and Port-au-Prince, *H.*

H. Bartlett 17714 (NY). Forêt des Pins-Savane Zombie road, *Imshaug & Wetmore 22806* (det. Crum; NY). Dépt. Sud'est, Savane Lage, road to Seguin, *Adams & Zanoni 11333*.—Crum and Steere (1958) reported several further Haitian collections. Elsewhere than Hispaniola, this beautiful species occurs in Cuba (Bizot, 1965) and Costa Rica.

Pireella mariae (Card.) Card. DOMINICAN REPUBLIC: Prov. de La Vega, near Los Tablones, 3 km west of La Ciénaga, alt. ca. 1200 m, *Norris, Gastony & Jones 5286* (det. Norris).—Until now, this species has been known only from Mexico and Central America, from Guatemala, Costa Rica, and Panama (cf. Arzeni, 1954).

Pleuridium holdridgei Crum & Steere was described from a single locality in the Mornes des Commissaires, Haiti (Crum & Steere, 1958), but it still is known elsewhere only from the Dominican Republic. Although this particular species is restricted to the West Indies, the genus as a whole is strongly continental in its general distribution over the world.

Pleurochaete luteola (Besch.) Thér. DOMINICAN REPUBLIC: Prov. Pedernales, 37 km north of Cabo Rojo, *Buck 4430*; 4 km south of El Aguacate, *Reese 15232*.—This easily recognized species has already been reported from Haiti by Thériot (1944) and by Crum and Steere (1958); it is known elsewhere from Cuba (Bizot, 1965), Mexico, Guatemala, Ecuador and Peru. Crum and Anderson (1981) have stated that they consider this species to be only a "robust expression" of *Pleurochaete squarrosa* (Brid.) Lindb., which has a wide distribution in the southern and southwestern United states, as well as around the world.

Pogonatum carionis (C. Müll.) Par. DOMINICAN REPUBLIC: Prov. La Vega, Alto de la Bandera, 2800 m, *Buck 5462*.—This continental species is known elsewhere only in Guatemala and Mexico.

Pogonatum leptopelma (C. Müll.) Par. DOMINICAN REPUBLIC: Prov. La Vega, vicinity of La Lagunita, alt. 2800 m, *Norris, Gastony & Jones 5549* (det. Norris).—Like the preceding, this species is otherwise known only from Guatemala and Mexico. Bartram (1949) said of it, "This appears to be a small edition of *P. robustum* without any sharply distinctive characters."

Pohlia cruda (Hedw.) Lindb. DOMINICAN REPUBLIC: Prov. Samaná, Honduras, *R. O. Schuster 45* (det. Judd).—This bipolar species is very common in northern North America and extends far southward in both the eastern and western mountain ranges; it occurs in Mexico and Central America and throughout the Andes of South America from Colombia to Chile and Patagonia, as well as to other parts of the Southern Hemisphere. It is also widespread in Europe and Asia. Nonetheless, this seems to be the first report for the West Indies.

Pohlia elongata Hedw. DOMINICAN REPUBLIC: Prov. La Vega, Pyramids site, alt. 7600 ft., *Reese 15771, 15772, 15775*; Alto de la Bandera, alt. 2800 m, *Buck 5466, Reese 15868, 15873, 15977, 15887*.—Widely distributed in southern Canada and the northern United States, extending far south in the mountains to Georgia and Arizona; also widespread in Europe and Asia. This typically continental species is apparently a new record for the West Indies.

Porotrichodendron bertrandii (Ren. & Card.) Broth. DOMINICAN REPUBLIC: Prov. Pedernales, above Los Arroyos, alt. 1640 m, *Smith 1014, 10153a*; Las Abejas, *Buck 4351, 4352, Reese 14971, Smith 10057a, 10059, Steere 22851, 22862*; south of El Aguacate, *Reese 15277*; north of Los Arroyos, *Steere 22902*. Prov. Peravia, La Nevera,

Reese 15724. Prov. Estrelleta, Sierra de Neiba, *Buck 4549, Reese 15141, 15149*.—This species was also reported from five localities in Haiti (Crum & Steere, 1958); elsewhere, it is known only from Mexico.

Porotrichodendron superbum (Tayl.) Broth. DOMINICAN REPUBLIC: Prov. La Vega, vicinity of Constanza, *Allard 16508, 17597b, 17688u*; Loma Campana, alt. 1036 m, *Allard 18382*; vicinity of La Lagunita, alt. 2600 m, *Norris, Gastony & Jones 5784A, 5777, 5792, 5793* (all det. Norris); Valle Nuevo-San José de Ocoa road, alt. 2300 m, *Norris, Gastony & Jones 7580*; 3 km west of La Ciénaga, *Norris, Gastony & Jones 5385* (all det. Norris). Prov. Peravia, La Nevera, *Liogier 21534, Mejía & Zanoni 8726*. Prov. Pedernales, Las Abejas, *Buck 4317, Reese 14957, Zanoni & Mejía 16817*. prov. La Estrelleta, north of Angel Feliz, Buck 4781, *Reese 15339*. HAITI: Dépt. Sud'est, 3 km west of Mare Rouge, road to Seguin, *Adams & Zanoni 11262, 11332, 11339*.—This continental species, which is known elsewhere in Guatemala, Costa Rica and South America, was reported from Haiti by Crum and Steere (1958).

Porotrichum plicatulum Mitt. DOMINICAN REPUBLIC: Prov. La Vega, vicinity of Piedra Blanca, *Allard 16675, 16683, 16687, 16929, 17836, 17861, 17871, 18147*; Loma Campana, *Allard 18433, 18491*; base of Loma Caribe, *Zanoni et al. 15766*, Prov. La Estrelleta, Sierra de Neiba, along Carretera Internacional, *Smith 10254*; Colonia Río Limpio, *Reese 15401, 15412, 15413*. Prov. Pedernales, Las Abejas, *Buck 4384, Reese 14936*; Mencia-Aguas Negras road, *Buck 4499*.—This species was originally described from Trinidad, whose flora has been derived essentially from South America, where it also occurs. Elsewhere, it is known from Mexico, Guatemala, and Costa Rica; it has been reported also from Puerto Rico (Crum & Steere, 1957).

Porotrichum squarrosum (Arzeni) Crum & Steere. [*Pireella squarrosa* Arzeni]. DOMINICAN REPUBLIC: Prov. La Vega, vicinity of Piedra Blanca, *Allard 16683, 16897, 16946, 18135*; Loma Campana, *Allard 18318, 18358, 18442, 18671, 18772*. Arzeni (1954) described *Pireella squarrosa* from two collections, one from Haiti (*Mackaness 99*, Savanne Zombi, type) and one from the Dominican Republic (*Allard 18382*, Loma La Campana). Crum and Steere (1958) reported a further specimen from Haiti, from Marmelade (*Nash s.n*; NY). This species is still known only from Haiti and the Dominican Republic; however, it will almost certainly be discovered in Central America or northern South America.

Pterobryon densum (Schwaegr.) Hornsch. DOMINICAN REPUBLIC: Prov. La Vega, vicinity of Constanza, *Allard 16556a, 17553a, 17588, Steere 22588, 22639*. Prov. San Rafael, Sierra de Neiba, Haitian border, alt. ca. 1400 m, *Norris, Gastony & Jones 6783, 6792* (both det. Norris). Prov. Pedernales, Las Abejas, *Steere 22937; Zanoni & Majía 16804A*. HAITI: Dept. l'Ouest, opposite Aniceto Martínez, *Reese 15371*.—This continental species is known elsewhere from Mexico, Guatemala, Costa Rica, Panama, northern South America, and Brazil; reported from Martinique by Welch and Crum (1970).

Ptilium orthothecium Thér.—Although *Ptilium* is a thoroughly continental genus which may eventually be found in the high-altitude pine forests of Hispaniola, it is not yet known to occur there. *Ptilium orthothecium* is, as noted by Judd (1980), only a synonym of *Hypnum polypterum* (Mitt.) Broth; I have verified Judd's conclusion through examination of an isotype specimen (*Ekman 1869*) at NY. Although Thériot (1944), in his original description, characterizes *P. orthothecium* as having "capsula erecta, cylindrica," it is in

fact suberect or even somewhat curved (as Thériot's illustration shows!), with a somewhat asymmetric mouth, much as in *Hypnum imponens*, although not so strongly so. The shortly acuminate leaves with conspicuous alar cells and an unusually well developed double costa are also typical of *Hypnum polypterum*.

Ptychomitrium lepidomitrium (C. Müll.) Schimp. in Besch. DOMINICAN REPUBLIC: Prov. La Vega, Alto de la Bandera near summit, alt. 2800 m, *Buck 5457, 5465, Reese 15872, 15874, 15876, 15844b, Steere 23096*; Valle Nuevo, *Steere 23058*.—Originally described from Mexico, this species, as well as the genus, are new to the West Indies. Although close to *P. serratum* B.S.G., this species is distinguished from it by the thickwalled leaf cells and the longer capsules. I am grateful to Howard Crum and Lewis Anderson for the identification.

Racomitrium crispulum (Hook.f. & Wils.) Hook.f. & Wils. DOMINICAN REPUBLIC: Prov. La Vega, Valle Nuevo, alt. 2680 m, *Jiménez M-77*; vicinity of La Lagunita, alt. 2800–2900 m, *Norris, Gastony & Jones 5531, 5586A, 5649* (all det. Norris); Constanza-Valle Nuevo road, alt. 2300 m, *Norris, Gastony & Jones 7080, 7512*; waterfall near Constanza, alt. 4000 ft., *Jones & Norris 1278*; Constanza-La Nuez road, alt. 5000–8000 ft., *Jones & Norris 1286A*; Valle Nuevo-San José de Ocoa road, alt. 2500 m, *Norris, Gastony & Jones 7609*; 3 km west of La Ciénaga, alt. 1200–1800 m, *Norris, Gastony & Jones 5392* (all det. Norris); Alto de la Bandera, alt. 2800 m, *Buck 5457, Reese 58992*.—This species has a very wide world distribution, always at high altitudes. In the Americas, it extends from Guatemala and Costa Rica southward through the Andes of South America to Fuegia; also in Indonesia, Malaysia, New Guinea, and Hawaii. Both genus and species are apparently new to the West Indies.

Racomitrium microcarpum (Hedw.) Brid. DOMINICAN REPUBLIC: Prov. La Vega, near summit, Alto de la Bandera, alt. 2800 m, *Smith 10324*.—This species has a very wide distribution in northern Europe, Asia, and North America; it appears to be new to Hispaniola and the West Indies.

Rhabdoweisia crispata (With.) Lindb. DOMINICAN REPUBLIC: Prov. La Vega, Pyramid site, *Reese 15771, 15774*.—This small moss has a wide but very spotty distribution in North and South America, Asia, Europe, and Indonesia; it seems to be new to the Antilles.

Rhacocarpus purpurascens (Brid.) Par. [*R. humboldtii* (Hook.) Lindb.]. DOMINICAN REPUBLIC: Prov. La Vega, Valle Nuevo-San José de Ocoa road, alt. 2500 m, *Norris, Gastony & Jones 7415, 7590*; vicinity of La Lagunita, alt. 2800–2900 m, *Norris, Gastony & Jones 5403, 5535, 5537* (all det. Norris); Alto de la Bandera, alt. 2800 rm, *Reese 15872*.—The geographic range of this beautiful moss includes Mexico, Central and South America, as well as Africa. It has long been known from the Lesser Antilles, from Guadeloupe, Dominica (Bartram, 1955), and St. Kitts, but it is new for the Greater Antilles.

Rhizogonium lindigii (Hampe) Mitt. DOMINICAN REPUBLIC: Prov. La Vega, waterfall, Constanza-Valle Nuevo road, alt. 1525 m, *Norris, Gastony & Jones 7491* (det. Norris).—This rather strongly continental species is known elsewhere in Guatemala, Costa Rica, Guayana, Colombia, and Brazil.

Rigodium toxarion (Schwaegr.) Schimp. DOMINICAN REPUBLIC: Prov. La Vega, Loma Campana, *Allard 18318*.—This species, originally described from the Dominican Republic, was also reported from three localities in Haiti by Crum & Steere (1958). It is

known otherwise from the Andes of South America, in Colombia, where it seems to be widespread, and Ecuador; Chile and Juan Fernández Islands.

Schistidium apocarpum (Hedw.) B.S.G. DOMINICAN REPUBLIC: Prov. La Vega, just below summit of Alto de la Bandera, alt. 2800 m, *Smith 10334 c. fr.*—This bipolar species is common and abundant in the colder parts of the world, as well as at higher altitudes towards the equator, from Mexico to Ecuador; apparently new to the West Indies.

Schistidium gracile (Röhl.) Limpr. DOMINICAN REPUBLIC: Prov. La Vega, Alto de la Bandera, alt. 2800 m, *Buck 5461, 5848, Reese 15867, 15881.*—Widely distributed in the northern parts of Europe, Asia, and North America, this species extends much farther south in the mountains in the United States; south to Mexico and Guatemala, but apparently new to the West Indies.

Sciaromium bartlettii Crum & Steere was originally described from collections from two localities in Haiti (Crum & Steere, 1958), but it has not yet been discovered in the Dominican Republic. However, it is included here because the genus is otherwise very definitely continental in its geographic distribution and does not occur elsewhere in the West Indies.

Taxiphyllum scalpellifolium (C. Müll.) Broth. DOMINICAN REPUBLIC: Prov. Dajabon, near El Pino, Río Hinaje, *Judd 1361, 1358* (det. Judd). Prov. Peravia, Río Yuna, Rancho Arriba, *Liogier 25733.*—A continental species known elsewhere from Mexico, Guatemala, Honduras, Nicaragua, and Costa Rica; first reported from Hispaniola and the West Indies by Judd (1980), on the basis of the specimens cited here.

Tortella richardsii Bartram. DOMINICAN REPUBLIC: Prov. Santiago, Pico Diego de Ocampo, alt. 1170 m, *Judd 1570* (det. Judd). Prov. Puerto Plata, Pico El Murazo, *Reese 15468.*—Known otherwise from British Honduras (Belize) and Guatemala; first reported from Hispaniola and the Antilles by Judd (1980), from his specimen cited here.

Tortella tortuosa (Hedw.) Limpr. DOMINICAN REPUBLIC: Prov. La Vega, Constanza-Valle Nuevo road, alt. 1615 m, *Judd 1292* (det. Zander).—This continental species has a very wide distribution in the northern part of North America, extending farther south in the mountains to Colorado, Tennessee, and North Carolina; also Guatemala. It was first reported from Hispaniola and the West Indies by Judd (1980), from his collection cited here.

Tortula fragilis Tayl. DOMINICAN REPUBLIC: Prov. La Vega, vicinity of Constanza, *Allard 17538b, 17588a, 17611a.*—This continental species is relatively rare in the mountains of the southern and southwestern United States, extending southward to Mexico and Guatemala; widespread in the Andes of South America from Colombia to Bolivia. First reported from the West Indies, from Haiti, by Crum and Steere (1958), from two localities.

Trichostomum brachydontium Bruch. DOMINICAN REPUBLIC: Prov. La Vega, near summit, Alto de la Bandera, alt. 2800 m, *Buck 5423, 5453, 5464, Reese 15869, 15888, 15889A, Smith 10334c* (det. Zander); Pyramid site, *Reese 15759.* Prov. Monte Cristi, Cabo del Morro, *Reese 15417, 15418, 15421.*—This continental species is widely distributed in Europe, Asia, and Africa; in North America, it seems to be restricted to Mexico and Guatemala. Bartram (1949) included Jamaica in his statement of the geographic range of this species, but in a later review of the mosses of Jamaica (Crum & Bartram, 1958), it is not mentioned. However, the collections cited here establish definitely its occurrence in Hispaniola and the West Indies.

Trichostomum tenuirostre (Hook . & Tayl.) Lindb. [*T. cylindricum* (Bruch) C. Müll.]. DOMINICAN REPUBLIC: Prov. La Vega, Valle Nuevo, *Liogier 24923* (det. Crum); Alto de la Bandera, alt. 2800 m, *Buck 5445, 5452, Reese 15879, 15885, Steere 23120*; La Culata, *Buck 5398, Reese 15840*; Pyramid site, *Steere 22687*. Prov. La Estrelleta, north of Angel Feliz, *Buck 4780, Reese 15338*. Prov. Peravia, La Nevera, *Steere 23080*. Prov. Pedernales, Las Abejas, *Steere 22920, 22953*; near Oviedo, *Buck 4439*.—This strongly continental species has a very wide but very spotty distribution in North America, from Greenland and arctic Alaska to Mexico, Guatemala and Costa Rica; also in the Andes of northern South America. This seems to be the first report from Hispaniola and the West Indies.

Zygodon campylophyllus C. Müll. [*Z. domingensis* Thér.]. DOMINICAN REPUBLIC: Prov. de la Vega, Alto de la Bandera, alt. 2800 m, *Buck 5451, Reese 15877, 15852. Steere 23100*.—Thériot described an Ekman collection (no. *13777*) from "Prov. de la Vega, Pico del Valle Nuevo, face of cliffs, 2,550 m." as a new species, *Z. domingensis* Thér. He also reported a collection from Haiti, from Morne de la Selle (*Ekman 3170*), as *Z. pentastichus* (Mont.) C. Müll., a Chilean species. According to Grout (1946) both of these reports should be referred to *Z. campylophyllus*. Crum and Steere (1958) also reported this species from several localities in Haiti, all at high altitudes. Other than Hispaniola, its distribution is strictly Central American, in Mexico and Guatamala.

Zygodon viridissimus (Dicks.) Brid. var. *rupestris* Lindb. ex C. J. Hartm. DOMINICAN REPUBLIC: Prov. Peravia, La Nevera, *Reese 15738*. Prov. Pedernales, Las Abejas, *Reese 14901, 14953*.—In these well developed specimens, the leaves are entire and the plants agree in other characters with *Z. viridissimus* instead of the much more common *Z. reinwardtii* (Hornsch.) A. Braun. This continental moss has a very wide but scattered distribution in the United States and Canada, and extends southward to Mexico; also widespread in Europe and Japan. This taxon does not seem to have been reported previously from Hispaniola or the West Indies.

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VARIATION AND TAXONOMY OF *WEISSIA* IN THE SOUTHWESTERN UNITED STATES. I. BIOMETRICAL ANALYSES[1]

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Abstract. Relationships were examined among ten taxa currently treated in the genus *Weissia* Hedw. from the southwestern United States. A biometrical approach was applied to the problems of variation in this complex. Clusters of morphologically similar plants were determined using a mixture of new characters and characters that had been used by earlier students of the group. The correspondence of these clusters to putative species was evaluated, and the extent of morphological intergradation among species was quantified. Techniques of multivariate analysis reduced complex relationships among taxa into more easily understood two- and three-dimensional associations without distortion of observable morphological patterns. There appear to be seven natural species within this complex: *Weissia andersoniana* Zander (= *W. glauca* Bartr.), *W. controversa* Hedw., *W. euteiches* Zander (= *W. tortilis* (Schwaegr.) C. Müll.), *W. hedwigii* Crum, *W. inoperculata* (Crum) Crum, Steere & Anderson, *W. jamaicensis* (Mitt.) Grout, and *W. ligulaefolia* (Bartr.) Grout.

In the southwestern United States, a remarkable pattern of speciation was discovered by Bartram (1927, 1928, 1931, 1945) in the genus *Weissia* Hedw. The complex of species that he described or reported as new to the United States is representative of the extremes in morphological variation that are associated with one of the most widespread and polymorphic genera of mosses. Bartram (1927) considered *Weissia* "to have evolved distinctive specific types to a much greater degree here than in any other part of the United States" and observed "we have practically no knowledge of the variability or geographical distribution of the plants comprising this group." This study examines relationships among ten taxa recognized in the genus *Weissia* (Crum et al., 1973) that are native to the western United States.

The majority of reports of the southwestern Weissias have come from southeastern Arizona and western Texas, areas which are part of the Mexican Highlands of the Basin and Range Province (Fenneman, 1946). It is in these desert mountains that differentiation or speciation in *Weissia* has occurred to a greater extent than is known elsewhere on the continent. The complex of species found in the Southwest is representative of the problems associated with *Weissia* since the early 19th century. Different members of the complex show alliances with *Hymenostomum* R. Br., *Astomum* Hampe, *Trichostomum* Bruch, or *Weissia*. Species delimitations are also problematical in this group. Many of the species closely resemble *Weissia controversa* Hedw., a widespread species notorious for its variability.

We applied a biometrical approach to these problems of variation within the southwestern species complex of *Weissia*. Morphological data were compared to chromosome

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number and behavior, anatomical features, and distributional patterns of each taxon to evaluate generic and species distinctions within the complex. Conclusions concerning taxonomic relationships are discussed elsewhere.

Materials and Methods. Ten species of *Weissia sensu lato* have been reported from the western United States. Five of the southwestern species are widespread, including two taxa described from Europe, *W. controversa* and *W. euteiches* Zander (= *W. tortilis* (Schwaegr.) C. Müll.; see Zander, 1985), and three species described by Bartram (1927) as endemic to the Southwest, *W. andrewsii* Bartr., *W. andersoniana* Zander (= *W. glauca* Bartr.; see Zander, 1985), and *W. ligulaefolia* (Bartr.) Grout. These five taxa are represented in the analyses by the largest numbers of samples. Of the five remaining species, two are known only from the type collections: *W. sweetii* Bartr. (Bartram, 1945) and *W. inoperculata* (Crum) Crum, Steere & Anderson (Crum, 1957). The latter is included in this study, although its type locality near Monterey Bay, California, is outside the geographical range of the southwestern species. A third species, *W. perligulata* Flow., described as endemic to Utah (Flowers, 1973), has also been reported from Colorado (Weber, 1973). *Weissia hedwigii* Crum and *W. jamaicensis* (Mitt.) Grout are rare in the Southwest. *Weissia hedwigii* has been reported from three localities in Texas (Whitehouse & McAllister, 1954; Prior, 1961), and *W. jamaicensis*, from four stations in Texas (Bartram, 1928; Whitehouse & McAllister, 1954; Magill, 1976) and one in Arizona (Grout, 1938).

Taxa that are neither native to the Southwest nor currently recognized in *Weissia* were included in some biometrical tests for comparison with possible relatives in the Southwest. *Weissia sharpii* Anderson & Lemmon, possibly derived from *W. controversa*, is a polyploid endemic to limestone outcrops in cedar barrens of the Cumberland Mountains and Interior Highlands (Anderson & Lemmon, 1973). *Trichostomum crispulum* var. *cucullatum* (Roth) Podp., a European taxon, was reported from Texas as new to North America (Redfearn, 1976). Gametophytic plants from this sterile collection were included for comparison with *W. jamaicensis* and *W. sweetii*, species reported to show affinities with *Trichostomum*. Plants of three North American species of *Astomum* also were included for comparison with *W. inoperculata*.

Populations of *Weissia sensu lato* in western Texas and southeastern Arizona were sampled intensively at different times from March 1978 to July 1979. Herbarium material was used in biometrical analyses for comparison with field collections or, in some cases, as the only material available for analysis. The numbers of collections sampled for each species varied. Detailed information on localities and field and herbarium collections included in analyses is given by Stoneburner (1981). Tests from the program packages, Statistical Analysis System (SAS, Helwig & Council, 1979) and Numerical Taxonomy System of Multivariate Statistical Programs (NT-SYS, Rohlf et al., 1977), were used to examine variation in morphological characters.

Morphological characters were chosen because of their traditional importance as key characters, their inclusion in published descriptions of the taxa, or the likelihood they might prove taxonomically useful. Sixty characters (Table 1) were tested initially for their usefulness in distinguishing among six groups of plants presumed to represent *W. andrewsii*, *W. controversa*, *W. andersoniana*, *W. ligulaefolia*, *W. hedwigii*, and *W. euteiches*. Ten plants representative of each taxon were included. Variation in each

TABLE 1. The results of an analysis of variance comparing the variability of 60 characters within (d.f. = 54) and among (d.f. = 5) taxa. Unless otherwise noted, leaf measurements refer to non-perichaetial leaves. Characters are grouped as follows: The first eleven are the ultimate set, and the first 32 are the penultimate set.

Character	F	Character	F
Leaf shape	3.46[c]	Number of lateral branches	0.17[a]
length	1.27[a]	Number of basal branches	0.50[a]
papillae height	18.88[e]	Leaf apex width	4.62[c]
papillae branching	57.63[e]	mucro cell number	3.56[c]
mucro length	8.55[e]	upper cell width	0.92[a]
costa width at base	13.17[e]	upper cell wall	0.57[a]
Capsule mouth width	10.69[e]	basal cell length	0.54[a]
Seta height	5.45[d]	basal cell width	0.69[a]
Peristome teeth < 10 μm	12.80[e]	basal cell wall	1.47[a]
teeth ≥ 10 μm	74.31[e]	Perichaetial leaf mucro	
Spore diameter	12.09[e]	length	5.73[d]
		apex width	3.64[c]
Plant height	1.97[a]	costa width	6.95[e]
Leaf width	7.48[e]	involution length	4.97[d]
width distance	2.54[b]	involution height	3.63[c]
width ratio	2.31[a]	involution width	2.78[b]
involution length	1.35[a]	involution cell number	7.80[e]
involution height	7.78[e]	involution ratio	3.20[c]
involution width	3.87[c]	upper cell length	3.31[c]
involution cell number	7.14[e]	upper cell width	3.03[b]
involution ratio	2.36[b]	Number of archegonia	0.36[a]
upper cell length	2.10[a]	Number of antheridia	0.48[a]
Guide cell number	2.79[b]	Capsule color	0.15[a]
Perichaetial leaf shape	2.20[a]	cell length	1.27[a]
width distance	2.62[b]	stomates	0.90[a]
length	3.52[c]	suboral height	1.01[a]
width	3.72[c]	Spore color	1.34[a]
Capsule length	5.27[d]	papillosity	0.57[a]
width	3.95[c]	Peristome	169.00[e]
width distance	4.57[c]		
shape	1.02[a]		
wall layers	2.81[b]		
cell width	3.31[c]		

[a]not significant.
[b]P < .05.
[c]P < .01.
[d]P < .001.
[e]P < .0001.

character was compared within and among taxa by one-way analysis of variance. A set of 32 characters was judged to have taxonomic value. The abilities of the 32 characters to discriminate among the taxa were tested by nested analysis of variance. Eleven taxa, the ten southwestern species and the eastern *W. sharpii*, were represented by 179 plants.

The correspondence of morphologically similar individuals, and the characters that define them, to the nominal species was tested by discriminant and factor analyses of the reduced character sets. Because it is frequently difficult in practice to distinguish whether individual plants are morphologically more similar to *W. controversa* rather than *W. andrewsii*, to *W. controversa* rather than *W. ligulaefolia*, or to *W. ligulaefolia* rather than *W. euteiches*, morphological similarities among plants were evaluated by a discriminant analysis, which assigned 530 plants measured for 11 characters to groups using a classification criterion. The plants were chosen from 325 field and herbarium collections representing the ten southwestern species and the eastern *W. sharpii*. Morphological

similarities of 469 plants measured for the set of 11 characters were examined by a principal axis factor analysis. Each of the plants was assigned to one of the five most common species in the Southwest.

Morphological similarity among individual taxa was evaluated by cluster and principal components analyses based on character means for each of the putative species. Phenograms generated by the programs reduced complex relationships into two or three dimensions that were more readily comprehended. A cluster analysis of the 11 species was performed on the means of 32 characters from 179 plants. To intensify dissimilarities among the taxa, a second analysis on an increased sample size included only the most critical characters. A cluster analysis of the 11 species was performed on the means of 11 characters from 457 plants. A principal components analysis also was performed on 11 character means for 457 plants from 11 species.

Prior to selecting plants for measurement, each clump, whether from a field or herbarium collection, was sprayed with water and allowed to rehydrate. Plants that appeared healthy and bore sporophytes were carefully removed from the soil and soaked in water until completely rehydrated. After dissection in water, the sporophyte and perichaetial and stem leaves were mounted separately in Hoyer's Solution (Anderson, 1954) for measurement. The manner in which characters were measured is given by Stoneburner (1981).

Results. Of the original 60 characters, those that proved to be more variable within than among taxa (non-discriminatory) or were correlated and functionally dependent or ontogenetically comparable (redundant) were excluded from further testing. For example, variation in the number of archegonia per plant was considered to be non-discriminatory, since variation in a group of plants judged to represent the same taxon was greater than variation among groups presumed to represent different taxa. Variation among taxa was significantly greater ($P \leq .05$) than within taxa for 38 characters (Table 1). Thirteen of these proved redundant, however, and were deleted. For example, the number of cells in the mucro of a leaf was considered a redundant character, because it is a mathematical function of the length of the mucro. Characters of the perichaetial leaves were correlated with those of the stem leaves. They were considered redundant, because they are serially homologous to stem leaves and appear to share a similar ontogeny. Traditionally, the two types of leaves have been described as little differentiated. In all, 32 characters were judged to have discriminatory value (Table 1). Seven of these characters did not show significant differences among taxa; they were retained, however, because of their traditional taxonomic importance. A nested analysis of variance of the 32 characters showed that 40% or more of the variation in only 15 characters could be explained by differences among species. Many of the characters that were shown to differ among species are useful in separating only the less common southwestern species and fail to discriminate among the problematical ones. A set of 11 characters was selected that could be considered most useful, on either traditional or statistical grounds, in distinguishing among taxa in the Southwest (Table 1).

The discriminant analysis reclassified 31% of the plants originally assigned to *W. andrewsii*, 29% assigned to *W. controversa*, 15% assigned to *W. andersoniana*, 10% assigned to *W. ligulaefolia*, and 18% assigned to *W. euteiches*. In the principal axis factor analysis, the first four factors accounted for 62% of the total variation in the group. The

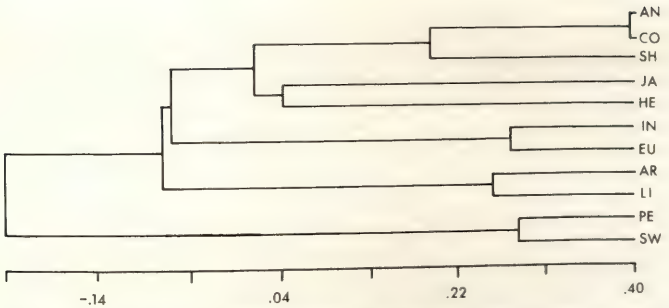

FIGURE 1. Phenogram expressing overall morphological similarity among 11 taxa of *Weissia*. The taxa are represented in this and succeeding figures by the first letters of the specific epithet or the generic name, except *W. andersoniana* as AR. UPGMA cluster analysis was based on the means of 32 characters from 179 plants. The cophenetic correlation coefficient is 0.648.

first factor explained 21% of the variation and was strongly influenced by mucro length, total leaf length, and the presence of developed teeth; the second factor explained 18% and was influenced by papillae branching and papillae height; the third factor accounted for 14% and was heavily loaded for costa width and capsule mouth width; and the fourth factor explained 9% and was influenced by the presence of rudimentary teeth. In a plot of factor one against factor two, four diffuse clusters of plants were recognized as comparable to *W. andersoniana, W. euteiches, W. ligulaefolia*, and *W. controversa–W. andrewsii*.

The phenogram based on 32 characters (Fig. 1) indicated close phenetic affinities between *Weissia andrewsii* and *W. controversa*. *Weissia sharpii, W. jamaicensis*, and *W. hedwigii* also were grouped with *W. controversa*. Relationships were posited for *W. inoperculata* with *W. euteiches, W. andersoniana* with *W. ligulaefolia*, and *W. perligulata* with *W. sweetii*. Using a similar data matrix with only gametophytic characters, a phenogram was generated that reflects the similarity of leaf characters in taxa with and without peristomes. The cophenetic correlation coefficients for the two cluster analyses were 0.648 and 0.673, respectively. The phenogram based on the set of 11 characters indicated that *W. andrewsii* is morphologically similar to *W. controversa* and *W. sharpii*, as is *W. hedwigii* to *W. inoperculata*. Using the same data set, but treating *W. wolfii* and *W. longiseta* as separate taxa from *W. controversa* and including plants of the genus *Astomum*, other relationships emerge (Fig. 2). While the affinities of *W. controversa* with *W. wolfii, W. longiseta, W. jamaicensis* and *W. ligulaefolia* are predictable, the relative isolation of *W. andrewsii* and *W. sharpii* from *W. controversa* is unexpected. The cophenetic correlation coefficients for the cluster analyses are 0.669 and 0.660, respectively. In a principal components analysis, the first three principal components or factors accounted for 72.5% of the variation. The first factor, which accounted for 33.9% of the variation, showed heavy loading for mucro length and spore diameter. The second factor, which accounted for 23.6% of the variation, showed heavy loading for leaf and seta length. The third factor, explaining 15.0% of the variation, was heavily influenced by

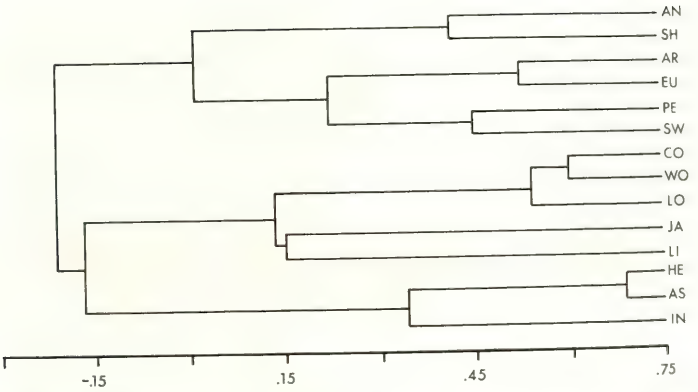

FIGURE 2. Phenogram expressing overall morphological similarity of 14 taxa of *Weissia*. UPGMA cluster analysis was based on the means of 11 characters from 462 plants. Plants of the type specimens of *W. longiseta* and *W. wolfii* are not included in *W. controversa*, but treated as separate taxa. Plants referable to the genus *Astomum* are also included. The cophenetic correlation coefficient is 0.660.

papillae height and leaf shape. The coordinates of the taxa on the first three principal axes are plotted in Figure 3.

Discussion. *Taxonomic Characters*—A large number of characters (60) were initially measured to increase the likelihood that taxonomically useful criteria would not be overlooked. Analysis of variance showed that more than half of the original characters demonstrated greater variation among groups than within groups. Based on statistical tests or traditional importance, 32 characters were judged to have some discriminatory value. Of these, less than one-half proved to be statistically critical in distinguishing among the taxa. A set of 11 characters was selected that either traditionally or statistically could be considered useful in distinguishing among taxa of *Weissia* (Table 1). Some of these characters, such as the length of the mucronate point, have not been regarded as critical by earlier workers. Certain other characters that have been considered important in delimiting taxa, such as the width of the costa, proved to be far less reliable. This points up the need for careful scrutiny of the characters employed in a taxonomic revision. Characters that have traditional importance may prove misleading, and more critical characters may be overlooked.

A number of previous studies also have concluded that statistical comparisons of the variation present in a large data base are an invaluable tool in understanding morphological relationships. MacLeod (1917), an early advocate of quantitative methods in bryophyte taxonomy, quantified variation in 12 leaf characters for ten species of *Mnium* Hedw. in Great Britain. He emphasized the difference between "gradation," or variation of a character along an axis, and individual variation. Greig-Smith (1954) quantified variation in 14 characters for 150 collections of *Lejeunea* Lib. in Great Britain and found

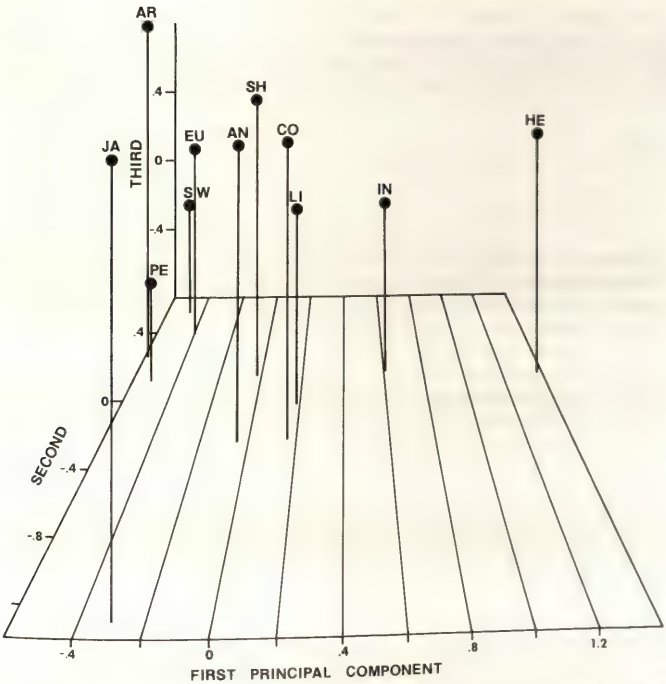

FIGURE 3. Three-dimensional plot resulting from a principal components analysis. Eleven taxa of *Weissia* are projected onto the first three principal axes using the means of 11 characters.

combinations of characters that distinguished among three taxa. Other innovative, univariate studies include a comparison of leaf characters among populations of subspecific taxa of *Plagiothecium micans* (Sw.) Paris (Redfearn, 1956). According to Redfearn, characters traditionally used to distinguish subspecies overlap significantly and are taxonomically unreliable. Lodge (1960), in a statistical comparison of leaf characters in plants from field populations and cultured clones of two species of *Drepanocladus* (C. Müll.) Roth, found that variation in leaf shape, cell length, and nerve width is environmentally induced and that the characters overlapped in the two taxa. He distinguished the two species by differences in angular leaf cells that were not environmentally modified. Briggs (1965) compared variation in leaf characters in plants from field populations and cultured colonies of four species of *Dicranum* Hedw. He found the species to be phenotypically plastic and recommended that varietal names be avoided. Koponen (1967) reported statistically significant differences in plants from a mixed population of *Mnium*

affine Funck and *M. medium* B.S.G. Hatcher (1967), using an elegant experimental design and univariate techniques, demonstrated genetic variation among clones of *Lophocolea heterophylla* (Schrad.) Dum. In a study of the *Brachythecium rutabulum* (Hedw.) B.S.G.–*B. rivulare* B.S.G. complex, Wigh (1975) compared morphological variation in the species under different environmental regimes and found that leaf length and costa length differ significantly between the two taxa. In an investigation of variation in leaf and cell characters within plants and among species of *Sphagnum* from the Atlantic Coastal Plain of North America, Lane (1981) found that *S. trinitense* C. Müll. cannot be distinguished from *S. cuspidatum* Hoffm. Habitat forms of *S. perichaetiale* Hampe, as well as two varieties of *S. imbricatum* Russ., were also morphologically inseparable. On the other hand, *S. fitzgeraldii* Ren. & Card. and *S. torreyanum* Sull. were shown to be distinct from *S. cuspidatum*.

Multivariate statistical methods have been used in a more limited way to describe patterns of variation in bryophytes. In an investigation of variation in *Pleuroclada albescens* (Hook.) Spruce, Szweykowski and Krzakowa (1967) found that dendritic methods produced results that supported the recognition of two varieties, as did an earlier treatment of the same data with scatter diagrams (Szweykowski & Krzakowa, 1966). Newton (1968) used factor analysis to show that morphological variation was continuous between two chromosome races of *Tortula muralis* Hedw. Seki (1968) delimited the family Sematophyllaceae in Japan using factor analysis. He evaluated species relationships within the family using discriminant analysis. Lefebvre and Lennes (1969) differentiated among seven species of *Plagiothecium* B.S.G. in Belgium with discriminant functions based on five quantitative characters. Smith (1970) showed, with principal components analysis, that two species of *Fissidens* Hedw. were morphologically inseparable. Rahman (1972) used this same technique to demonstrate that 87 collections of *Sphagnum subsecundum* scored for 23 characters corresponded either to var. *inundatum* (Russ.) C. Jens. or var. *auriculatum* (Schimp.) Schlieph. He recommended treating the taxa as varieties rather than species, because discriminant analysis showed that in practice a significant number of the samples were difficult to classify. In an investigation of closely related species of *Ulota* Mohr ex Web., Smith and Hill (1975) used correspondence analysis, an analogue of principal components analysis that is appropriate for discrete data, to examine variation in four qualitative and six quantitative characters that were converted to qualitative variables. According to Smith and Hill, *U. bruchii* Hornsch. and *U. crispula* Bruch should be included in *U. crispa* (Hedw.) Brid. Hill and Smith (1976) were dissatisfied with that approach and recommended a method that combines principal components analysis and correspondence analysis for biosystematic studies with both quantitative and qualitative characters. Principal components analysis showed that morphological variation in *Sphagnum rubellum* Wils. in Britain intergraded to such a degree with *S. capillaceum* (Weiss) Schrank that Hill (1976) concluded the former did not even merit varietal status. In a principal components analysis of variation in bulbils of *Pohlia proligera* (Kindb. ex Limpr.) Lindb. ex Arnell, Lewis and Smith (1977) found that certain genetic differences demonstrated in culture could not be detected in field populations. Cluster analyses (Wyatt & Stoneburner, 1981) of *Donrichardsia macroneuron* (Grout) Crum & Anderson and closely related species in *Amblystegium* B.S.G. and *Eurhynchium* B.S.G. supported the treatment of *Donrichardsia* as a monotypic genus.

Similarity of individuals—Multivariate tests that compare the morphological similarity of individuals indicated that morphological intergradation is prevalent among certain taxa of *Weissia* in the Southwest. There is disparity in the percentages of plants reclassified by discriminant analysis. The greatest proportion of reclassification occurred between *W. andrewsii* and *W. controversa* and between *W. euteiches* and *W. ligulaefolia*. In many instances the reclassified plants reflected errors in original determinations of the collections. Re-examination of the specimens in question frequently resulted in a revised understanding of the taxa. Thirty-five of the 325 populations (11%), however, were considered sufficiently intermediate in nature between *W. ligulaefolia* and *W. controversa–W. andrewsii* or *W. ligulaefolia* and *W. euteiches* that it was considered likely they were either mixtures or interspecific hybrids.

The principal axis factor analysis indicated that plants fall into fairly well-defined groups based on those characters that contribute to factors one and two: mucro length, leaf length, presence of developed teeth, and papillae height and branching. The clusters of plants are not discrete, but overlapping. *Weissia andersoniana* is apparently the most distinctive taxon, and *W. controversa* and *W. andrewsii* overlap most broadly. The boundary between *W. ligulaefolia* and *W. euteiches* is not well-defined, nor is the boundary between *W. ligulaefolia* and *W. controversa*. The greatest amount of intergradation occurs between *W. andrewsii* and *W. controversa* and between those taxa and *W. ligulaefolia*. Intergradation occurs to a lesser degree between *W. ligulaefolia* and *W. euteiches*. *Weissia andersoniana* and the less common species in the complex are relatively well-differentiated taxa.

Similarity of taxa—Cluster and principal components analysis are considered complementary tests of morphological affinity (Rohlf, 1970). According to Rohlf, cluster analysis provides an estimate of the similarity of closely related taxa, while principal components analysis estimates relationships among more distantly related taxa. The former is useful for exploring the fine structure of relationships, while the latter provides a picture of the overall structure of a complex. The phenogram generated by a cluster analysis based on 32 characters underscored the close relationship between *W. andrewsii* and *W. controversa*. *Weissia sharpii, W. jamaicensis*, and *W. hedwigii* were grouped with *W. andrewsii* and *W. controversa*, taxa with which they share a similar leaf morphology. *Weissia sweetii* and *W. perligulata* were shown to be morphologically similar. A phenogram generated by a cluster analysis of a similar data matrix using only gametophytic characters illustrated the taxonomic confusion that results from determinations of barren or poorly fruiting southwestern material. A comparison of phenograms based on cluster analyses of the set of 11 characters demonstrates that it is necessary to include all related taxa for a thorough understanding of a species complex. The relative isolation of *W. andrewsii* and *W. sharpii* from *W. controversa* is produced when taxa more similar to *W. controversa* are recognized in the analysis, the vars. *longiseta* and *wolfii*. The close relationship posited for *W. hedwigii*, the genus *Astomum*, and *W. inoperculata* can be understood in terms of the reduction of the sporophyte. Again, *W. perligulata* is shown to resemble closely *W. sweetii*. Collections of *W. euteiches* are frequently mistaken for those of *W. andersoniana*, and the morphological similarity of the species is indicated by cluster analysis.

Results of principal components analysis showed that *W. hedwigii, W. jamaicensis*, and

W. andersoniana are clearly distinguished from their congeners. *Weissia controversa*, *W. andrewsii*, and *W. sharpii* are closely associated. The eperistomate species are morphologically more similar to certain peristomate species than to each other. *Weissia ligulaefolia* resembles *W. controversa* to a greater extent than it does *W. euteiches*, and *W. euteiches* demonstrates strong affinities with *W. sweetii* and *W. andersoniana*.

Morphological studies, supported by other lines of evidence, indicate that *W. andrewsii* should be considered conspecific with *W. controversa* and that *W. sweetii* and *W. perligulata* also represent members of a single species and should be synonomized under *Trichostomum crispulum*. *Weissia andersoniana*, *W. hedwigii*, *W. jamaicensis* and *W. euteiches* appear to be distinct species. *Weissia ligulaefolia* is one of the more variable of the southwestern species, intergrading with both *W. controversa* and *W. euteiches*. There is some evidence that this intergradation is the result of hybridization. The morphological relationship of *W. inoperculata* with the genus *Astomum* supports the inclusion of it and other astomous species in *Weissia*.

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CHEMOSYSTEMATICS OF THE MNIACEAE. I. IDENTITIES OF LOWRY'S SPECIES PAIRS[1]

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Abstract. Prior to presenting evidence from flavonoid analysis regarding the phylogeny and taxonomy of the Mniaceae, it is necessary to clear up the confusion surrounding Lowry's (1948) species pairs. This confusion exists because of numerous nomenclatural and taxonomic changes in the names for taxa within the family since Lowry's publication. Of the 25 specimens studied by Lowry, 23 were located and borrowed from MICH. These and two additional cytological vouchers that were not cited in Lowry's paper were determined using recent taxonomic treatments. The haploid-autodiploid species pairs proposed by Lowry therefore are: *Mnium ambiguum–M marginatum, Plagiomnium cuspidatum–P. cuspidatum, P. ellipticum–P. medium*, and *Rhizomnium punctatum* subsp. *chlorophyllosum–R. pseudopunctatum*.

The Mniaceae is an acrocarpous family of mosses in the Bryales distinguished by their broad leaves with short cells and inclined, symmetrical capsules with a double peristome. They are frequent and abundant on soil in mature hardwood forests of the temperate Northern Hemisphere and range northward into boreal and arctic regions. The family comprises a natural group that can be subdivided easily into a number of subgroups, which have been recognized at various taxonomic ranks by different authors. Koponen's (1968–1980) revisionary studies of the family recognized about 71 species in 10 genera. By way of comparison, Crum and Anderson (1981) distinguished the same total number of taxa (23) in eastern North Americas Koponen, but they placed these in two genera and 20 species in contrast to Koponen's six genera and 23 species. The number of real taxonomic entities is therefore not in question, but rather the status which these should be accorded.

The name *Mnium* dates back to Dillenius (1741) and was used by Linnaeus (1753) to include three hepatics, causing much nomenclatural confusion (Evans, 1907). Hedwig's (1801) concept of *Mnium* included 13 species, only five of which are presently included in the Mniaceae. By the time of Bruch, Schimper, and Gümbel (1838), the taxonomy of the European species had stabilized, and most subsequent activity involved the discovery of new species in remote areas and the recognition of generic and subgeneric groups. Lindberg (1868) segregated *Trachycystis* and *Leucolepis* from *Mnium*, and this trend of splitting *Mnium* into separate genera continued through 1957 when Holmen (1957) described *Cyrtomnium* and 1980 when Bowers (1980*a*) segregated *Stellariomnium*. The treatment of genera by Koponen (1968) is derived basically from the views of Limpricht (1895), Kindberg (1897), Loeske (1910), and Kabiersch (1936), although these earlier authors recognized these groups at the rank of subgenera or sections. In subsequent work,

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Koponen has arranged the more closely related species within the three largest genera into 2–5 sections. These sections also were preceded by similar groupings in the taxonomic schemes of Kindberg (1897) and Kabiersch (1936).

Koponen's generic concepts have met with a mixture of strong praise and strong criticism. While most European taxonomists have followed Koponen's lead in recognizing segregate genera such as *Plagiomnium* and *Rhizomnium* (e.g. Smith, 1978b), many bryologists elsewhere have steadfastly resisted the elevation of these sections to genera (e.g. Scott & Stone, 1976; Crum & Anderson, 1981). Crum and Anderson (1981) accept generic status for *Cinclidium* and *Leucolepis* in North America but stress the "evolutionary continuity within the complex" to explain their rejection of the more recent segregates. In their opinion, "chipping away at a broadly conceived genus may be justified up to a point, but it eventually becomes difficult to know where to stop." This view is illustrated by the elevation of *Mnium stellare* and its two closest relatives successively from the rank of subsection (Kindberg, 1897) to section (Koponen, 1968) to genus (Bowers, 1980a).

More substantial disagreements than those surrounding taxonomic ranks in the Mniaceae involve Koponen's use of certain characters in constructing phylogenetic trees, using the cladistic methodology of Hennig (1950, 1966). His treatment of *Rhizomnium* (Koponen, 1973), for example, places primary emphasis on the presence or absence of micronemata. These non-axillary rhizoids were ignored by earlier taxonomists working on the Mniaceae and played no role in their phylogenetic schemes. Koponen's reliance on rhizoid topography produces a picture of relationships that contrasts sharply with the traditional one generated by overall morphological similarity. *Rhizomnium appalachianum*, which is very similar to *R. punctatum* and often treated as a variety of that species, is placed very early into a different group from *R. punctatum*. Similarly, *R. andrewsianum* and *R. gracile*, which can scarcely be separated at all morphologically (Steere, 1978), are widely isolated from each other in Koponen's (1973) scheme.

Another evolutionary trend within certain of the major groups in the Mniaceae has generated controversy recently. This is the phenomenon of "species pairs," first proposed by Lowry (1948) on the basis of chromosome counts. The species pairs consist of a haploid progenitor and a derived autodiploid, presumably the product of apospory. The Mniaceae includes numerous examples of such processes, and these have frequently been discussed in literature reviews of cytology and repoductive biology (e.g. Smith, 1978a, 1979; Anderson, 1980; Wyatt, 1982; Wyatt & Anderson, 1984). In the Mniaceae the haploid taxa are typically dioicous, while the autodiploids are monoicous (Lowry, 1948; Mogensen, 1973), as in *Atrichum* (Lowry, 1954) and many other groups (Wyatt, 1984). Bowers (1969a), however, reported that *Mnium saximontanum*, an autodiploid presumably derived from *M. arizonicum*, is dioicous. Koponen (1974), in rejecting *M. saximontanum* as insufficiently distinct from *M. arizonicum* to represent a separate species, used the holotype of *M. saximontanum* to represent his concept of *M. arizonicum*. Wyatt and Anderson (1982) pointed out that autodiploid taxa are more likely to be accorded status as species when the doubling event leads to a change in sexuality. Even so, *Plagiomnium cuspidatum*, which is known to consist of both haploid-dioicous and diploid-monoicous races (Lowry, 1948; Andrews, 1959) is commonly treated as a single species. There apparently are no obvious morphological traits associated with ploidy condition in *P. cuspidatum*.

Lowry's (1948) classic study of species pairs in the Mniaceae has been criticized by Mogensen (1973) and by Koponen and Nilsson (1977). On the basis of morphological and cytological evidence, Mogensen (1973) suggested that monoicous *Cinclidium stygium* is indeed derived by autopolyploidy from dioicous *C. arcticum*. However, *Cinclidium subrotundum*, another monoicous diploid, is not closely related to *C. latifolium*, a dioicous haploid widely assumed to be the progenitor of *C. subrotundum*. Furthermore, Mogensen (1973) does not rule out the possibility of allopolyploidy in the origin of some diploid taxa of the Mniaceae. Koponen and Nilsson (1977) argued on morphological grounds that many of Lowry's (1948) proposed species pairs were erroneous and suggested alternative haploid progenitors for each of the autodiploids.

Recognizing that the morhpological data are ambiguous in establishing relationships in this complex, Koponen and Nilsson (1977) employed chemical evidence to test their hypotheses concerning species pairs. Unfortunately, their chemosystematic evidence is fraught with problems. In addition to a number of methodological oversights, they failed to present most of their evidence, and the data they do report are ambiguous with respect to the question of likely progenitors. Their conclusions are based solely on "spot patterns"; no attempt was made to identify the actual flavonoids. At most only two or three collections of selected taxa were analyzed. No samples of certain other potential progenitors were analyzed. The authors allude to "difficulties in reproducing the experimental conditions" and state that they "used only the information obtained by studying the patterns of the main components." Furthermore, it is apparent from their single figure, presenting chromatograms of *Plagiomnium insigne* and *P. medium*, that not all of their "spots" represent flavonoids, but rather simpler phenolic acids (D. E. Giannasi, personal communication). Insufficient data are presented to evaluate most of their arguments regarding the species pairs, in spite of which Koponen and Nilsson (1977) reach conclusions such as "*P. affine* obviously differs significantly from *P. medium* in its flavonoid content, which may be taken as an argument against the suggestion that they constitute a pair." It should be apparent that the real usefulness of flavonoid analysis in addressing taxonomic problems in the Mniaceae has not been tested.

In collaboration with Ann Stoneburner, David M. Lane, David E. Giannasi, James R. Manhart, and others, I have therefore undertaken a comprehensive study of the flavonoid chemistry of the Mniaceae. This approach provides an independent test of the proposed phylogeny of the group, allowing critical evaluation of its present taxonomy. We are using flavonoid profiles to "fingerprint" taxa and thereby resolve questions regarding progenitor-derivative relationships among haploid and autodiploid species pairs. The rationale for such an approach has been summarized by Crawford and Levy (1978): "In many instances, flavonoids are useful taxonomically because plants viewed as members of the same species on morphological considerations exhibit identical or very similar profiles whereas plants otherwise treated as distinct species often have detectably different falvonoid arrays. Taxon-specific flavonoids also provide biochemical fingerprints/markers which may indicate the genomic origins of hybrid and polyploid taxa." To verify our conclusions regarding the most likely progenitor of a given autodiploid species, we are synthesizing autodiploids through apospory (Crum, 1973; Anderson, 1980).

Because of the large number of nomenclatural and taxonomic changes in the Mniaceae, it is impossible in some cases to be certain exactly which taxa, according to recent classifications, Lowry (1948) studied and intended as species pairs. The purpose of this

paper is therefore to re-examine Lowry's voucher specimens and determine precisely which taxa were analyzed.

Materials and Methods. Vouchers from Lowry's (1948) cytotaxonomic study of the Mniaceae were deposited in the Herbarium at the University of Michigan (MICH). These were borrowed and their appropriate names determined according to Koponen's (1968, 1969, 1971, 1972, 1973, 1974, 1980), Mogensen's (1973), and Bowers's (1980b) taxonomic treatments. Permanent mounts in Hoyer's Solution were made for each species and comparisons were made with authentic collections, including material from MICH, DUKE, NY, and the private herbarium of A. Stoneburner and R. Wyatt.

Results and Discussion. Through correspondence with H. Crum, R. J. Lowry, and E. A. Phillips, a total of 25 specimens were accumulated. These represented 23 of the 25 specimens reported by Lowry (1948). Two of the original 25 specimens could not be located for determination. In addition, there were among the specimens from MICH two collections that were not listed by Lowry (1948), but which did represent cytological vouchers of taxa in the Mniaceae. The identities of each of the 25 specimens I examined are listed in Table 1 and discussed in the sections below.

Mnium.—*Mnium marginatum* was postulated by Lowry (1948) to represent the autodiploid derivative of *M. orthorrhynchum*. Because the latter is a taxonomic synonym of *M. thomsonii*, it has been generally assumed that Lowry's species pair in this group was actually *M. thomsonii–M. marginatum* (Koponen & Nilsson, 1977). Koponen and Nilsson (1977) criticized this hypothesis and suggested, alternatively, that *M. marginatum* was derived from "*M. lycopodioides* or one of its relatives, *M. ambiguum, M. laevinerve*, or *M. umbratile*." It is possible that Lowry (1948) and Koponen and Nilsson (1977) are in agreement, since Lowry's voucher (4) of *M. orthorrhynchum* actually represents *M. ambiguum*. Although Lowry (1948) discussed only one collection (3) of *M. marginatum*, there is a second specimen (14b) at MICH for which a diploid chromosome number was found. These and other collections of *Mnium, M. stellare* (1, 22, 23), *M. hornum* (24), and *M. spinulosum* (8), were found to be correct as determined. According to the taxonomic classification proposed by Bowers (1980a, 1980b), *M. stellare* would be *Stellariomnium stellare* (Hedw.) M. C. Bowers.

Plagiomnium.—Within section *Rosulata* (Kindb.) Kop. of *Plagiomnium* are one diploid (*P. medium*) and six haploid species. Lowry (1948) hypothesized that *M. medium* is an autodiploid derived from *M. affine*. Koponen and Nilsson (1977) suggested, alternatively, that *P. insigne* is the proper haploid to pair with *P. medium*, stressing the morphological similarity of the two. Since *P. insigne* was studied by Lowry (1948), Koponen and Nilsson (1977) expressed surprise at his choice of *M. affine* "as the mother species of *P. medium*." In fact, Lowry's (1948) vouchers (9, 10, 18) of *M. affine*, a species that Koponen (1971) excluded from North America, are of the segregate species *P. ellipticum*. A fourth specimen (16) studied by Lowry (1948) could not be located, but probably it also represents *P. ellipticum*. These same conclusions were reached independently by Koponen, who examined the avialable specimens at MICH in 1977 (Koponen & Nilsson, 1977). The correct species pair according to Lowry's cytological study is therefore *P. ellipticum–P. medium*.

Lowry's (1948) vouchers (7, 12, 25) of *P. medium* all represent subsp. *medium* of *P. medium*. His specimen (5) of *P. insigne* is likewise representative of that taxon. Contrary

TABLE 1. Identities of the 25 cytological vouchers at MICH deposited by Lowry (1948). When the name used in the paper differs from the determination on the specimen, the former is noted in parentheses.

Collector	Voucher	Orignial determination according to Andrews (1940)	Current designation according to Koponen (1968–1980)
Lowry	1	*Mnium stellare* Reich.	*Mnium stellare* Hedw.
Lowry	2	*Mnium punctatum* (L.) Hedw.	*Rhizomnium punctatum* (Hedw.) Kop. subsp. *chlorophyllosum* (Kindb.) Kop.
Holdridge	3	*Mnium marginatum* (Dicks.) P.-Beauv.	*Mnium marginatum* (With.) P.-Beauv.
Lowry	4	*Mnium orthorhynchum* Brid.	*Mnium ambiguum* H. Müll.
Svihla	5	*Mnium insigne* Mitt.	*Plagiomnium insigne* (Mitt.) Kop.
Svihla	6	*Mnium menziesii* (Hook.) C. Müll.	*Leucolepis acanthoneura* (Schwaegr.) Lindb.
Lowry	7	*Mnium medium* B.S.G.	*Plagiomnium medium* (B.S.G.) Kop. subsp. *medium*
Lowry	8	*Mnium spinulosum* B.S.G.	*Mnium spinulosum* B.S.G.
Lowry	9	*Mnium affine* Bland in Schwaegr. (var. *ciliare* C. Müll.)	*Plagiomnium ellipticum* (Brid.) Kop.
Lowry	10	*Mnium affine* Bland in Schwaegr.	*Plagiomnium ellipticum* (Brid.) Kop.
Lowry	11	*Mnium cinclidioïdes* Hüb.	*Pseudobryum cinclidioïdes* (Hüb.) Kop.
Lowry	12	*Mnium medium* B.S.G.	*Plagiomnium medium* (B.S.G.) Kop. subsp. *medium*
Schornherst	13	*Mnium cuspidatum* (L.) Leyss.	*Plagiomnium cuspidatum* (Hedw.) Kop.
Phillips	14a	*Mnium cuspidatum* (L.) Leyss.	No specimen
Lowry	14b	*Mnium marginatum* (Dicks.) P.-Beauv.	*Mnium marginatum* (With.) P.-Beauv.
Lowry	15	*Mnium drummondii* Bruch & Schimp. in Hook.	*Plagiomnium drummondii* (Bruch & Schimp.) Kop.
Lowry	16	*Mnium affine* Bland in Schwaegr.	No Specimen
Lowry	17	*Mnium punctatum* (L.) Hedw. var. *elatum* Schimp. (*M. pseudopunctatum* Bruch & Schimp.)	*Rhizomnium pseudopunctatum* (Bruch & Schimp.) Kop.
Lowry	18	*Mnium affine* Bland in Schwaegr.	*Plagiomnium ellipticum* (Brid.) Kop.
Lowry	19	*Mnium cuspidatum* (L.) Leyss.	*Plagiomnium cuspidatum* (Hedw.) Kop.
Sanbourne	20	*Mnium punctatum* (L.) Hedw. (*M. glabrescens* Kindb.)	*Rhizomnium glabrescens* (Kindb.) Kop.
Lowry	21a	*Cinclidium stygium* Sw.	*Cinclidium stygium* Sw.
Lowry	21b	*Mnium punctatum* (L.) Hedw. (var. *elatum* Schimp.)	*Rhizomnium pseudopunctatum* (Bruch & Schimp.) Kop.
Lowry	22	*Mnium stellare* Reich.	*Mnium stellare* Hedw.
Lowry	23	*Mnium stellare* Reich.	*Mnium hornum* Hedw.
Blomquist	24	*Mnium hornum* L.	*Plagiomnium medium* (B.S.G.) Kop. subsp. *medium*
Lowry	25	*Mnium medium* B.S.G.	

to his statement in the paper, however, specimen 9 is clearly to be assigned to *P. ellipticum* and not *P. ciliare*.

Plagiomnium cuspidatum exists as both a dioicous, haploid race and a more common synoicous, diploid race (Lowry, 1948; Andrews, 1959). Because the races do not differ consistently in morphology, they have traditionally been treated as a single species. Lowry's (1948) study included both haploid (14a, 19) and diploid (13) populations, and he supposed that the two represented an intraspecific haploid-autodiploid pair. Bowers (1969b), however, proposed that synoicous *P. cuspidatum* represents an autopolyploid of *P. acutum*, a dioicous, haploid species of eastern Asia. Koponen and Nilsson (1977) agreed with Bowers's hypothesis, although their data do not support such a relationship. Lowry's voucher 19 is undoubtedly *P. cuspidatum*. His other specimen (14a) of diploid *P. cuspidatum* could not be located, and his collection 13 of the haploid race from Florida was sterile. All erect shoots of the specimen had been dissected or eaten so that they could not be sexed to confirm the dioicous condition. The vegetative characters of the sample, however, fit well within the range of variation typical for *P. cuspidatum*. The voucher (15) of *P. drummondii* was correctly determined.

Rhizomnium.—*Rhizomnium* section *Rhizomnium* includes one diploid (*R. pseudopunctatum*) and 12 haploid taxa. Lowry (1948) proposed *R. punctatum* (including in the broad sense of Andrews (1940): *R. appalachianum, R. punctatum* subsp. *punctatum, R. punctatum* subsp. *chlorophyllosum*, and *R. magnifolium*) as the most likely progenitor of *R. pseudopunctatum*. Koponen and Nilsson (1977), on the other hand, argued strongly that *R. gracile* is "the most probable, and from the morphological point of view the only possible, candidate." They also pointed out that Brassard (1974) was in error in citing Koponen's (1973) work as suggesting that *R. andrewsianum* is the progenitor of *R. pseudopunctatum*.

The specimen (2) cited by Lowry (1948) as "typical, dioicous *Mnium punctatum*" represents a mixed collection, consisting mostly of *R. punctatum* subsp. *chlorophyllosum* but containing a few shoots of *R. magnifolium*. It is apparent, therefore, that Lowry's chromosome studies were of *R. punctatum* subsp. *chlorophyllosum* and that he considered this taxon the most likely progenitor of *R. pseudopunctatum*. His other specimens represent either *R. pseudopunctatum* (17, 21b) or *R. glabrescens* (20).

Additional Taxa.—Although no other species pairs were proposed, Lowry (1948) did study material of three additional genera. He discovered an apparent diploid number for *Cinclidium stygium*. His determination of that specimen (21a) is consistent with recent taxonomic treatments (Koponen, 1969; Mogensen, 1973). This is also true for Lowry's (1948) material of *Leucolepis acanthoneura* (6) and *Pseudobryum cinclidioides* (11). Bowers (1980b) argued on cytological grounds that the segregate genus *Pseudobryum* is doubtfully distinct from *Plagiomnium*, hence this taxon was listed as *Plagiomnium cinclidioides* (Hüb.) M. C. Bowers in his taxonomic scheme.

It is hoped that this review of the species pairs proposed in the Mniaceae will clear up misunderstandings about Lowry's (1948) work that have resulted from the numerous nomenclatural and taxonomic changes in names for taxa of the Mniaceae. From examination of Lowry's (1948) original material, it is apparent that he hypothesized the following haploid-autodiploid species pairs: *Mnium ambiguum–M. marginatum, Plagiomnium cuspidatum–P. cuspidatum, P. ellipticum–P. medium*, and *Rhizomnium puncta-*

tum subsp. *chlorophyllosum–R. pseudopunctatum*. In subsequent work, my co-workers and I propose to test these hypothesized relationships by analysis of variation in flavonoid chemistry.

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NOMENCLATURAL TRANSFERS IN *WEISSIA* (POTTIACEAE, MUSCI)

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Abstract. *Astomum phascoïades* (Hook. ex Drumm.) Grout, *Hyophila microcarpa* (Schimp.) Broth. and *Hymenostomum semidiaphanum* Thér. are transferred to *Weissia*, in which genus new names are necessarily provided for the first two: *Weissia phascopsis* nom. nov. and *W. minycarpa* nom. nov., respectively. The combination *W. semidiaphanum* (Thér.) comb. nov. made for the third, *Weissia andersoniana*, nom. nov., is furnished for *W. glauca* Bartr., hom. illeg., and *W. euteiches* nom. nov. for *W. tortilis* (Schwaegr. in Schrad.) C. Müll., hom. illeg.

Study of the family Pottiaceae for contribution of treatments of some genera for the proposed moss flora of Mexico, edited by A. J. Sharp, has shown the necessity for several nomenclatural novelties. Four new names and a new combination are given in this paper for species of *Weissia sensu lato* (including *Astomum* and *Hymenostomum* as sections).

Weissia andersoniana nom. nov.

Weissia glauca Bartr., Bryologist 30: 80. 1927, replaced synonym, hom. illeg. non *W. glauca* (Hedw.) Arnott.

The new name is given in honor of Dr. Lewis E. Anderson, and recognizes a long and distinguished career as teacher and researcher in North American bryology.

The distinctive characters of *W. andersoniana* are the whitish leaves, the "V" shape of differentiated basal cells, and the "antleroid" upper laminal papillae. *Weissia semidiaphana* may have highly spiculose upper laminal papillae that are almost as highly developed as are those of *W. andersoniana*. Although *W. semidiaphana* has a less strongly differentiated "V" of basal cells, certainty of identification requires fruiting material: *W. andersoniana* is peristomate while *W. semidiaphana* is aperistomate.

Weissia euteiches nom. nov.

Gymnostomum tortile Schwaegr. in Schrad., Neu. Bot. Jour. 4: 17. 1810, replaced synonym.

Hymenostomum tortile (Schwaegr. in Schrad.) B.S.G., Bryol. Eur. 1: 56. 1846 (fasc. 33–36 Mon. 6).

Weissia tortilis (Schwaegr. in Schrad.) C. Müll., Syn. Musc. 1: 661. 1849, hom. illeg. non *W. tortilis* Spreng., 1827.

This species is found in western U.S.A., Mexico, Central America, Brazil, Europe, northern Africa and the Caucasus. It differs from *W. controversa* in its broader, usually

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oblong-lanceolate leaves with less tightly incurved or involute margins, somewhat broader costae, 50–70 μm wide near the base, peristome always lacking, and the thecal walls 3–4 cell layers thick. *Weissia euteiches* is usually autoicous, but, in Mexico, some specimens were seen that were both autoicous and synoicous on the same plant, or paroicous and synoicous within the same collection. *Weissia controversa* occasionally has similarly thick thecal walls, but is usually peristomate.

Weissia minycarpa nom. nov., non *W. microcarpa* Hook. F. & Wils., 1859.

Trichostomum microcarpum Schimp. ex Besch., Ann. Sci. Nat. Bot., sér. 6, 3: 198. 1876, replaced synonym.

Hyophila microcarpa (Schimp.) Broth., Nat. Pflanzenf. 1(3): 403. 1902.

This species is known from Mexico, Guatemala, the West Indies, and Venezuela. The gametophyte of *W. minycarpa* has much the appearance of small forms of *Trichostomum brachydontium* Bruch in F.A. Müll., while the sporophyte is similar to those of species of *Astomum*, being rotundiform and lacking a peristome. It is possible that this and some other species presently recognized in *Hyophila* might prove to have the same relationship to *T. brachydontium* as species of *Weissia* sect. *Astomum* and *W.* sect. *Hymenostomum* have to *W.* sect. *Weissia*. For example, one specimen of *Hyophila subangustifolia* from Venezuela: Distrito Rangel, *Griffin 902* (BUF, FLAS) has the narrow, aperistomate capsule mouth and thick exothecial walls of 3–4 layers of cells characteristic of at least some species of sect. *Hymenostomum*, while its gametophyte is indistinguishable from that of *T. brachydontium*. The peristome of *T. brachydontium* itself is quite variable, ranging from linear teeth to rudimentary plates. If parallel series of reduction in peristome development were found in *Weissia* and *Trichostomum*, a convenient distinction between the genera might be had in the degree of inflexion of the upper leaf margin: *Trichostomum* having plane to broadly channelled leaves while *Weissia* has sharply or at least strongly incurved leaf margins. Until more work is done on these genera, however, aperistomate and monoicous species with rather small gametophytes are better left in *Weissia*.

Weissia phascopsis nom. nov., non *W. phascoïdes* (B.S.G.) C. Müll., 1851.

Gymnostomum phascoïdes Hook. ex Drumm., Musci Amer. (Rocky Mts.) no. 12, 1828, replaced synonym.

Astomum phascoïdes (Hook. ex Drumm.) Grout, Moss Fl. N. Amer. 1(3): 152. 1938.

Hymenostomum rostellatum var. *phascoïdes* (Hook. ex Drumm.) Card., Bull. Herb. Boissier 7: 317. 1899.

Weissia rostellata var. *phascoïdes* (Hook. ex Drumm.) Reese & Lemmon, Bryologist 68: 282. 1965.

As pointed out by Crum and Anderson (1981), this widespread species is unrelated to *Weissia rostellata* (Brid.) Lindb., which differs in its plane leaf margins, poorly differentiated perichaetial leaves, and elongate capsules. The collection reported by G. Juárez G. and A. J. Sharp (1976) as new to Mexico (as *W. rostellata* var. *phascoïdes*) is not that but is instead *W. semidiaphana*.

Weissia semidiaphana (Thér.) comb. nov.

Hymenostomum semidiaphanum Thér., Smiths. Misc. Coll. 85(4): 5. 1931, basionym.

This species is endemic to Mexico, and is only weakly distinguishable from *W. phascopsis*. The seta of *W. phascopsis* is 1.5–2.0 mm long and the leaves reach the base of the capsule when they are wet and extended. The seta of *W. semidiaphana* is, however, 0.5–3.2 mm long and the leaves usually do not reach the base of the capsule when wet and extended. *Weissia semidiaphana* also has elliptical to ovate capsules, while those of *W. phascopsis* are ovate to subspherical.

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A FURTHER ELECTROPHORETIC STUDY OF PEROXIDASE ISOENZYME VARIATION IN *PELLIA EPIPHYLLA* (L.) DUM. FROM POLAND, WITH SPECIAL REFERENCE TO THE STATUS OF *PELLIA BOREALIS* LORBEER[1]

ROMAN ZIELINSKI[2] JERZY SZWEYKOWSKI[2], AND EWA RUTKOWSKA[2]

Liverworts are characterized, in general, by the very stable chromosome number, $n=9$, realized in over 90 percent of the species studied. Relatively rare are numbers $n=8$ and $n=10$, and polyploid series of $n=9$, 18, 27 . . . are exceptional (Fritsch, 1972; Smith, 1979; Schuster, 1966), the polyploid plants being morphologically very similar to the monoploid ones.

In 1934, G. Lorbeer discovered an 18 chromosome form of the bisexual *Pellia epiphylla* that showed only minor differences in the cell size. Specific status was given to this form, which was accordingly named *Pellia borealis* Lorbeer (1934). This has been questioned by later authors (Grolle, 1976; Szweykowski & Koźlicka, in preparation).

Because of a great morphological similarity, or even identity (Mendelak, 1972), there is a general belief among authors that *Pellia borealis* is an autoploid derivative of *P. epiphylla* (see e.g. Smith, 1979). However, Jachimsky (1935) discovered that the chromosomes of both forms in question show differences in size and distribution of heterochromatin. According to this author, *Pellia borealis* could come into being in result of hybridization of *P. epiphylla* with a second, unknown species of the genus. However, according to Paton and Newton (1967) these differences could be a result of a long evolution. Szweykowski and Mendelak (unpublished) measured the lengths of the whole chromosome sets in the both chromosomal forms, i.e. $n=9$ and $n=18$, and showed that the length of the chromosome set in *P. borealis* is significantly less that twice its length in *P. epiphylla*. The relation of these lengths is 1:1.6.

Szweykowski, Zieliński and Mendelak (1981) studied variation of peroxidase isoenzymes in both forms. They discovered interesting differences and expressed the opinion that although autopolyploidy cannot be ruled out, the situation is much more complicated as it seemed to be. We present now additional facts concerning this problem.

Material. Pellia species grow usually gregariously, forming systems of groups comprising very different numbers of thalli. Such groups are called colonies (Anderson & Lemmon, 1974; Szweykowski, Odrzykoski & Zieliński, 1981). Plants were collected from natural populations (for the population sites see appendix, page 208), according to two different procedures:

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1. In most populations only one fragment of one colony amounting to ca. 25 square centimeters was taken. From each sample, three separate thalli were isolated randomly and were cloned subsequently on a peat layer in a plastic cuvette; 75 populations were sampled in that manner.

2. Seven of these populations mentioned above were sampled more thoroughly: 15 to 81, depending on the size of population, colonies were sampled as above. Only one thallus per colony, i.e. per sample, was cloned subsequently.

Methods. Living thalli were assayed cytologically with respect to their chromosome numbers and electrophoretically to reveal the peroxidase isoenzyme banding patterns. Each clone was studied with both methods, except for some samples coming from big populations sampled according to the second procedure above. Thus we have an absolute correlation between chromosome numbers and peroxidase isoenzyme patterns.

1. Cytological methods. Chromosome numbers were determined in all 75 populations sampled. Growing apices of cloned thalli were pretreated with 0.3 percent solution of 8–hydroxychinoline for 4 hours at +12°C and fixed in acetic ethanol (1:3) for 24 hours. After hydroloysis in 1N HCl for 9 minutes at +60°C, the tissues were stained with acetohaematoxyline.

2. Electrophoresis. Electrophoretic isoenzyme assays were performed on all clones coming from all populations sampled. It means that at least three clones, i.e. three different thalli, per population were assayed. Electrophoresis was performed as described previously (Szweykowski, Zieliński & Mendelak, 1981) except that the paper wicks used to absorb the crude extracts of the thalli were wider (ca. 8mm). This allowed for obtaining more distinct band patterns.

Results

1. The occurence of *Pellia epiphylla* sens. str. (i.e. $n = 9$ plants) and *P. borealis* (i.e. $n = 18$ plants) in Poland. Since the description of *Pellia borealis* as a separate species in 1934, the plant has been considered rare in Central Europe (see e.g. Müller, 1954). Mendelak (1972) was the first to forward the opinion that the $n = 18$ form, i.e. *P. borealis*, is much more widespread, at least in Poland, than it was thought to be.

Our new data confirm this opinion. Out of 75 *Pellia epiphylla* sens. lat. populations (i.e. populations of monoicous plants) 46 comprised only $n = 18$ plants, 23 only $n = 9$ plants, and at six stations both forms were found. Thus, *Pellia borealis* is about twice as frequent in Poland as *P. epiphylla* sens. str.. It grows both in northern and in southern parts of the country (Fig. 1). However, *Pellia epiphylla* sens. str. seems to be more frequent in lower elevations of the Tatry Mts. (southern Poland).

2. Mixed populations. In six populations both forms, i.e. $n = 9$ and $n = 18$, were found growing together. Four were investigated more thoroughly, i.e. according to the procedure described under 2 above. In all cases one of the two forms was dominant, the second being only a small admixture (Table 1), its frequency being less than 5 percent. In two cases *P. epiphylla* was the dominant form (populations no. 205 and 272), in two others (nos. 274 and 285) *P. borealis* dominated. This situation is interesting because according to the data obtained by M. Mendelak and D. Dorociak (unpublished) populations of *Pellia epiphylla*

FIGURE 1. The geographical distribution of *Pellia epiphylla*, 1, and *P. borealis*, 2, in Poland.

sens. str. comprising polysomatic thalli with singular $n = 18$ cells are by no means rare. The frequency of such polysomatic plants in two more thoroughly investigated populations was around 5.10^{-2}.

3. Peroxidase variability.

3.1. Comparison of peroxidase isoenzyme patterns in *Pellia epiphylla* and *P. borealis*. As has been shown earlier (Szweykowski, Zieliński & Mendelak, 1981), one can distinguish two different zones of activity in peroxidase isoenzyme patterns in all European *Pellia* species studied so far. The slower zone, staining as a homogenous, broad band, and the faster zone, comprising several distinct bands. Three different peroxidase phenotypes differing in the faster zone band patterns were discovered in *Pellia epiphylla* sens. str. They were designated PX1, PX2, and PX3. *Pellia borealis* showed only two phenotypes, which seemed to be identical with phenotypes PX1 and PX2 of *Pellia epiphylla*.

However, our new results show that this identity was only apparent. By using little modified electrophoresis parameters we were able to show distinct, although small, differences in band patterns of *Pellia borealis* and *P. epiphylla* (Fig. 2). Therefore, we

TABLE 1. Distribution of particular peroxidase phenotypes in 75 *Pellia* populations studied.

Population number	Peroxidase phenotypes *Pellia epiphylla* $n=9$ PX1[a]	PX2[a]	PX3	*P. borealis* $n=18$ PX1[b]	PX2[b]
20	–	–	–	+	–
21	–	–	–	–	+
43	–	–	–	+	–
44	–	–	–	–	+
45	–	–	–	+	–
50	–	–	–	+	–
75	–	+	–	–	–
86	–	+	–	–	–
87	–	+	–	–	–
88	–	+	–	–	–
92	–	–	–	+	–
94	+	–	–	–	–
105	–	+	–	–	–
110	–	–	–	–	+
124	–	–	–	+	–
131	–	–	–	+	+
135	–	–	–	+	+
139	–	–	–	+	–
140	–	–	–	+	–
146	–	+	–	–	–
154	–	–	–	–	+
156	–	–	–	+	–
157	–	–	–	+	–
159	–	–	–	–	+
160	–	–	–	–	+
165	–	–	+	–	–
169	–	–	–	+	+
171	–	+	–	–	–
172	–	+	–	–	–
175	–	+	–	–	–
178	–	+	–	–	–
180	–	+	–	–	–
189	+	+	–	–	–
190	+	+	–	+	–
192	–	–	+	–	–
197	–	–	–	–	+
199	–	–	–	–	+
203	–	–	+	+	–
204	–	–	–	+	–
205	–	–	+	–	–
206	–	–	–	–	+
208	–	–	–	+	–
209	–	–	–	–	+
210	–	–	–	–	+
212	–	–	–	+	+
214	–	–	–	+	–
215	–	–	–	–	+
217	–	–	–	–	+
219	–	–	–	–	+
220	–	–	–	–	+
221	–	+	–	–	–
222	–	+	–	–	+
224	–	+	–	–	+
225	–	+	–	–	+
233	–	–	+	–	–
234	–	–	–	+	–
235	–	–	+	–	–
236	–	–	–	–	+
237	–	–	–	–	+
238	–	–	–	–	+
240	–	–	–	–	+
242	–	–	–	–	+
243	–	–	–	–	+
245	–	–	–	–	+
246	–	–	–	+	+
248	–	–	–	+	–
265	–	+	–	–	–
287	–	+	–	–	–
296	–	+	–	+	+
297	–	–	–	+	–
299	–	+	–	–	–
300	–	+	–	–	–
305	–	–	–	–	+
310	–	–	–	–	+
321	–	–	–	+	–

have changed the symbols of these phenotypes to PX1[a] and PX2[a] in *Pellia epiphylla* and to PX1[b] and PX2[b] in *P. borealis*.

The differences between phenotypes PX1[a] and PX1[b] are two-fold: first, the central band of the faster zone migrates a little further in *P. borealis* (PX1[b]) than in *P. epiphylla* (PX1[a]). Secondly, the electrophoretic lanes are distinctly stained when assayed in *P. borealis* plants, thus the bands are seen against a colored background. This is not the case with *P. epiphylla*. The differences between PX2[a] and PX2[b] are, in a sense, even more pronounced. *Pellia borealis* shows two distinct bands in the lower part of the faster zone, whereas *P. epiphylla* shows invariably only one band in this region. Also the background of the gel lane is intensively more darkly stained in *P. borealis* than in *P. epiphylla*.

As can be seen, the differences are small but, nevertheless, they are of consequence. On the basis of many hundreds of thalli studied we express now the opinion that both

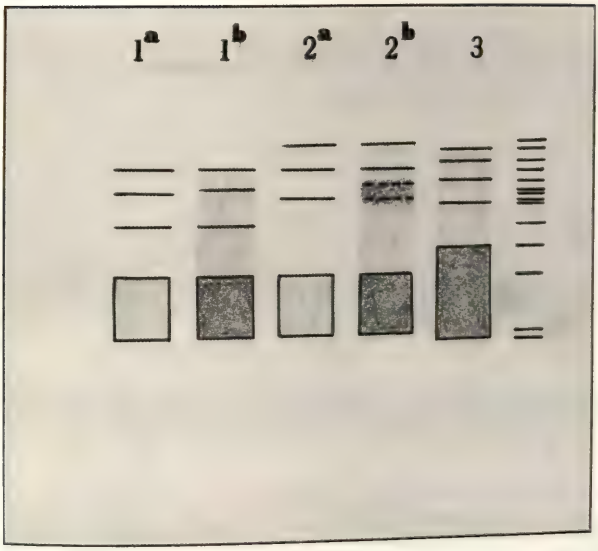

FIGURE 2. Diagrammatic representation of peroxidase band patterns discovered in *Pellia epiphylla*, 1^a, 2^a and 3, and in *P. borealis*, 1^b and 2^b. On the right side bands found in all Pellia taxa studied so far.

plants, i.e. *P. borealis* and *P. epiphylla* proper, differ in their peroxidase isoenzyme patterns. One thing must be stressed, however: the respective phenotypes $PX1^a$ and $PX1^b$ on one side and $PX2^a$ and $PX2^b$ on the other are much more similar within pairs, i.e. $PX1^a$ to $PX1^b$ and $PX2^a$ to $PX2^b$, than across them.

The third isoenzyme phenotype observed in *Pellia epiphylla*, i.e. PX3, has no counterpart in *P. borealis*. In fact, the differences between this phenotype and the remaining two are much more pronounced than those between $PX1^a$ and $PX2^b$. Not only are all the bands of the upper (faster) zone unique for this phenotype—there is no band in common with the remaining two phenotypes—but also the lower band, which is identical in $PX1^a$ and $PX2^a$, is much longer here (Fig. 2). The similarities between the five phenotypes discussed, i.e. $PX1^a$, $PX2^a$, $PX1^b$, $PX2^b$ and PX3, are shown in the Fig. 3.

3.2. Frequencies of particular phenotypes in *P. epiphylla* and *P. borealis*. As has been shown earlier (Szweykowski, Zieliński & Mendelak, 1981), the particular peroxidase phenotypes differ in their occurence as far as their frequencies are concerned.

The majority of *Pellia epiphylla* populations are composed of the phenotype $PX2^a$ in southern Poland (22 populations) and of the phenotype PX3 in northern Poland (6 populations). The phenotype $PX1^a$ is very rare: it has been found until now in one station in the Sudetes (populations 189 and 190) and in the Tatry Mts. (population 272). In the last place the $PX1^a$ phenotype comprises 13 percent of colonies sampled.

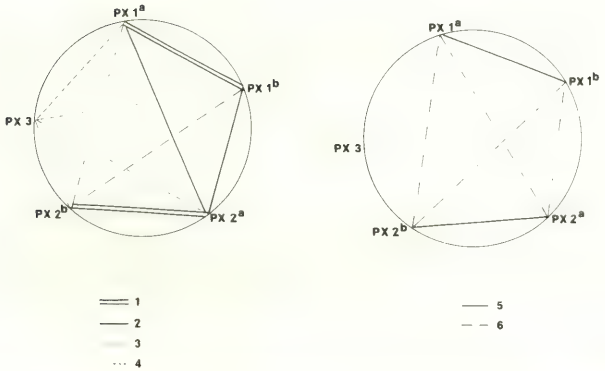

FIGURE 3. Diagrammatic representation of similarity between particular peroxidase phenotypes as expressed by simple matching coefficients S_{sm}, left, and Jaccard's coefficients of similarity, S_j, right.—1. $S_{sm}>0.80$.—2. $0.70<S_{sm}<0.80$.—3. $0.60<S_{sm}<0.70$.—4. $S_{sm}\leq 0.60$.—5. $S_j>0.50$.—6. $0.00<S_j<0.50$.

Both phenotypes of *Pellia borealis*, i.e. $PX1^b$ and $PX2^b$, are about equally frequent. They grow in some populations together and, in addition, with *Pellia epiphylla*. The structures of six mixed populations are shown in the Table 2.

3.3. The geographical distribution of particular phenotypes (Fig 4–6).

3.3.1. *Pellia epiphylla*, $n=9$ (Fig 4–5). There is a distinct geographical differentiation between the PX3 phenotype and the two remaining ones. The former grows exclusively in northern Poland, whereas the latter in Southern Poland only. The single population from Sweden we studied showed PX3 pattern.

3.3.2. *Pellia borealis*, $n=18$ (Fig 5–6). There are no such clearcut differences in the geographical distribution of the peroxidase phenotypes $PX1^b$ and $PX2^b$—both seem to be growing in the whole Polish territory. However, most stations of the $PX2^b$ are localized in the south Polish hill region, at lower mountain elevations, and at the highest parts of the moraine landscape in northern Poland. On the contrary, the $PX1^b$ phenotype grows in northern Poland mainly outside of the moraine top region and in the foothills of the Sudetes (southwestern Poland). The clarification of this issue demands further work, not only in Poland.

Discussion

On the basis of the results presented above, some problems seem to be worthy of being discussed at some length.

4.1 The first problem is that of the mutual relations between *P. epiphylla* and *P. borealis*. Both forms turned out to be different as far as their peroxidase phenotypes were concerned. However, as the differences are rather small (see Fig. 2 and 3), it cannot be

TABLE 2. Structure of seven more thoroughly sampled *Pellia* populations.

Population number	Thalli assayed	Peroxidase phenotypes, %					n = 9 thalli = *P. epiphylla*, %	n = 18 thalli = *P. borealis*, %
		1[a]	2[a]	3	1[b]	2[b]		
205	30	—	–	96.7	3.3	—	96.7	3.3
265	21	—	100.0	—	—	—	100.0	–
272	66	12.1	83.1	—	—	4.8	95.2	4.8
274	81	—	1.2	—	3.7	95.1	1.2	98.8
284	23	-	—	—	65.2	34.8	—	100.0
285	27	—	3.8	—	33.3	62.9	3.8	96.2
286	15	—	—	—	53.3	46.7	—	100.0

FIGURE 4. The geographical distribution of three peroxidase phenotypes PX1[a], PX2[a], PX3 of *Pellia epiphylla*, $n = 9$, in Poland.

TABLE 3. Frequency of particular peroxidase phenotypes in 75 Polish *Pellia* populations.

Phenotype	Present in *n* populations	%	Species
$PX1^a$	3	6.9	*Pellia epiphylla*, $n = 9$
$PX2^a$	22	72.4	
PX3	6	20.7	
$PX1^a$	25	42.3	*P. borealis*, $n = 18$
$PX2^b$	33	57.7	

taken as the evidence against the autopolyploid origin of *Pellia borealis*. It seems, thus, that our arguments published in the last paper (Szweykowski, Zieliński & Mendelak, 1981) still hold.

These arguments were concerned with problems that arise if such an autopolyploid origin of *P. borealis* were accepted. According to the paper cited above, there were four problems of that kind.

4.1.1. We have to accept at least two independent polyploidization routes: from $PX1^a$ to $PX1^b$ and from $PX2^a$ to $PX2^b$. The differences between patterns of $n = 9$ plants, i.e. $PX1^a$ and $PX2^a$, and those of $n = 18$ plants, i.e. $PX1^b$ and $PX2^b$, could be the effect of the changed gene dosage, or they could originate during the long evolution period after the polyploidization.

4.1.2. The different geographical distribution of the five peroxidase phenotypes shows that *P. borealis* in northern Poland either migrated from the south where both $PX1^a$ and

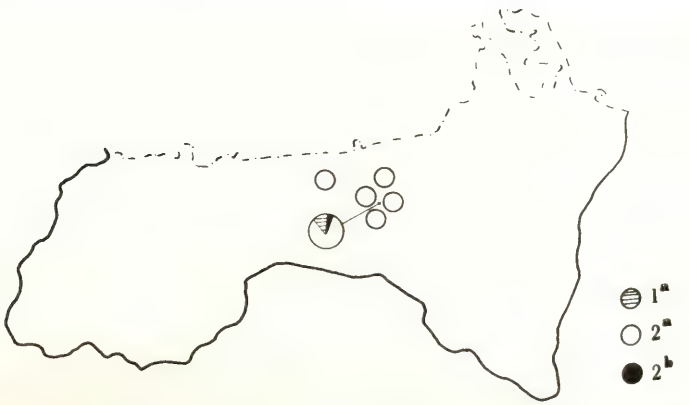

FIGURE 5. The geographical distribution of *Pellia* phenotypes in the Tatry Mts.—$1^a = PX1^a$.—$2^a = PX2^a$—*Pellia epiphylla*, $n = 9$.—$2^b = PX2^b$—*Pellia borealis*, $n = 18$.

FIGURE 6. The geographical distribution of two peroxidase phenotypes, $PX1^b$ and $PX2^b$, of *Pellia borealis*, $n = 18$, in Poland.

$PX2^a$ are growing presently, or, if it originated in the north, then these two phenotypes must have occurred there in the past and subsequently become extinct.

4.1.3. One of the *Pellia epiphylla* phenotypes, namely $PX1^a$, is a very rare plant, at least in Poland, whereas the second one ($PX2^a$) is rather frequently found in the southern parts of our country. On the contrary, both polyploid derivatives, i.e. $PX1^b$ and $PX2^b$, grow in the whole country with nearly equal frequencies. This discrepancy argues for the change of adaptive value of the $PX1^a$ plants after becoming polyploids.

All these three issues (4.1.1., 4.1.2., and 4.1.3) argue for *P. borealis*'s being an old polyploid.

4.1.4. Mendelak (Szweykowski, Zieliński & Mendelak, 1981) and Dorociak (unpublished data) discovered the presence of $n = 18$ cells in thalli of *P. epiphylla* ($n = 9$ chromosomes in most cells). This fact of polysomaty and also the occurrence of mixed populations comprising both $n = 9$ and $n = 18$ plants show that the possibility of the recent origin of *P. borealis* cannot be ruled out.

These results show that much work is still needed to reach a satisfactory solution of the problem of the origin of *P. borealis*. The present status of our knowledge, however, points

rather to the notion that *P. borealis* is an old polyploid plant and that the recent polyploidization, if any, plays a minor role in the evolution of *Pellia epiphylla–P. borealis* complex.

An additional problem to be mentioned here is the taxonomic status of *Pellia borealis*. As is well known, it has been reduced to a mere synony of *Pellia epiphylla* (Grolle 1976). However, in the light of the differences discovered in the peroxidase phenotypes and all the facts described under the heading 4.1., we express the opinion that it is still premature to solve the taxonomic problem in this way. It would be better, for the time being, to maintain the specific status for *Pellia borealis*, if it is only to save the problem of its origin falling into oblivion.

Finally, there exists the problem concerning the northern Polish phenotype PX3 of *Pellia epiphylla*. As it has been shown, it differs sharply in its geographical distribution, and the differences in the peroxidase phenotypes seem to be profound, too. Especially, the lower, i.e. the slower, band which is usually monomorphic within species, is unique here. One can have doubts whether this form belongs to the *Pellia epiphylla* gene pool.

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Appendix. Populations sampled.

Explanation of abbreviations. names of collectors: I.G. = Iwona Gasser; W.K. = Władysław Kola; B.K. = Bożena Kwiatkowska; M.M. = Maria Mendelak; I.O. = Ireneusz Odrzykowski; W.P. = Wiesław Prus-Głowacki; L.U. = Lech Urbaniak; J.S. = Jerzy Szweykowski; R.Z. = Roman Zielinski. (PX)-peroxidase phenotypes.

Pellia epiphylla, $n = 9$. 75,-Babia Gora, Plaj, leg. I.G.., 1975 (2^a); 86,-Wisła, Nowa Osada, leg. M.M., 1975 (2^a); 87,-Wisła, Czarne, leg. M.M., 1975 (2^a); 88,-Wisła, Nowa Osada, leg. I.G., 1975 (2^a); 94,-Boczań, Tatry, leg. J.S., 1976 (1^a); 105,-żawoja Policzna, Babia Góra, leg. L.U., 1976 (2^a); 146,-Bieszczady, Berežki-Przysłup, leg. M.M., 1978 (2^a); 165,-Linówek, peat bot., leg. M.M., 1978 (3); 171,-Beskid Żywiecki, Rajcza, leg. B.K., 1978 (2^a); 172,-Żawoja, Babia Góra, leg. B.K., 1978 (2^a); 175,-Stok Wysokiego, Tatry, leg. J.S., 1978 (2^a); 178,-Boczań, Tatry, leg. J.S., 1978 (2^a); 180,-Stok Wysokiego, Tatry, leg. R.Z., 1978 (2^a); 189,-waterfall, Karkonosze, leg. R.Z., 1978 (1^a, 2^a); 190,-waterfall, Karkonosze, leg. R.Z., 1978 (1^a, 2^a); 192,-Kampinos near Warszawa, leg. M.M., 1978 (3); 203,-Miłomłyn near Ostróda, leg. M.M., 1979 (3); 205,-Pestkownica near Kuźnica Żelichowska, leg. M.M., 1979 (3); 221,-Rabka, Gorce, Mts, leg. I.O., 1979, (2^a); 222,-Odrzykoń near Krosno, leg. I.O., 1979 (2^a); 224,-Nowy Targ fabryczny, leg. J.S., 1979 (2^a); 225,-Kowaniec, leg. I.O., 1979 (2^a); 233,-Kampinos, reserve, leg. M.M., 1980 (3); 235,-Klembów near Warszawa, leg. M.M., 1980 (3); 265,-Dolina Białego, Tatry, leg. J.S., 1980 (2^a); 287,-Rajcza, leg. M.M., 1979 (2^a); 296,-Ojców, reserve, leg. R.Z., 1981 (2^a); 299,-Karłów, leg. W.G., 1981 (2^a); 300,-Karłów, leg, W.G., 1981 (2^a).

Pellia borealis, $n = 18$. 20,-Duszniki, Góry Bystrzyckie, leg. M.M., 1974, (1^b); 21,-Duszniki, Góry Bystrzyckie, leg. M.M., 1974 (2^b); 43,-Sulistrowiczki, Masyw Ślęży, leg. M.M., 1974 (1^b); 44,-Masyw Ślęży, leg. M.M., 1974 (2^b); 45,-Wilkowo near Trzebnica, leg. W.K., 1975 (1^b); 50,-Rościsławice, Wzgórza Trzebnicko-Ostrzeszowskie; leg. M.M., 1974 (1^b); 92,-Duszniki,-Góry Bystrzyckie, leg. J.S., 1976 (1^b); 110,-żawoja Lajkonik, Babia Góra, leg. L.U., 1976 (2^b); 124,-Diabli Skok Wielki, reserve, leg. M.M., 1978 (1^b); 131,-Karłów, Góry Stołowe, leg. M.M., 1978 (1^b, 2^b); 135,-Czarna Woda, stream, near Sulistrowiczki, Wrocław, leg. M.M., 1978 (1^b, 2^b); 139,-Zieleniec, Góry Orlickie, leg. W.P., 1978 (1^b); 140,-Tychnowy near Kwidzyń, leg. J.S., 1978 (1^b); 154,-Bór na Czerwonym, Nowy Targ, leg. M.M., 1978 (2^b); 156,-Kamień lake, near Miastko, leg. M.M., 1978 (1^b); 157,-Koczała near Słupsk, leg. M.M., 1978 (1^b); 159,-Koczała near Słupsk, leg. M.M., 1978 (2^b); 160,-Wieczywno Małe lake, leg. M.M., 1978 (2^b); 169,-Snieżnik, leg. E.S., 1978 (1^b, 2^b); 190,-Szklarka waterfall, Karkonosze Mts, leg. R.Z., 1978 (1^b); 197,-Piekielna Dolina, Góry Bystrzyckie, leg. B.K., 1979 (2^b); 199,-Sulistrowiczki near Wrocław, leg. M.M., 1979 (2^b); 203,-Ruskie lake near Ostróda, leg. M.M., 1979 (1^b); 204,-Ostróda near Olsztyn, leg. M.M., 1979; 206,-Osowo Lęborskie near Słupsk, leg. M.M., 1979 (2^b); 208,-Miechucino near Gdańsk, leg. M.M., 1979 (1^b); 209,-Trątkownica near Gdańsk, leg. M.M., 1979 (2^b); 210,-Żaganiec near Żagań, leg. J.S., 1979 (2^b); 212 Warta Bolesławicka, Bolesławiec, leg. J.S., 1979 (1^b, 2^b); 214,-stream between Wejherowo and Kartuzy, leg. J.S., 1979 (1^b); 215,-Ostrowiec near Sławno, leg. J.S., 1979 (2^b); 217,-Ludźmierz, Kotlina Nowotarska, leg. J.S., 1979 (2^b); 219,-Nowy Targ, leg. J.S. 1979 (2^b); 220,-Nowy Targ Fabryczny, leg. J.S., 1979 (2^b); 222,-Odrzykoń near Krosno, leg. I.O., 1979 (2^b); 224,-Nowy Targ Fabryczny, leg. J.S., 1979 (2^b); 225,-Kowaniec, leg. I.O., 1979 (2^b); 234,-Kąty Borucza near Mińsk Mazowiecki, leg. M.M., 1980, (1^b); 236,-Góry Swiętokrzyskie, leg. J.S., 1980 (2^b); 237,-Syców near Ostrzeszów, leg. J.S., 1980 (2^b); 238,-Grabice, Góry Swiętokrzyskie, leg. J.S., 1980 (2^b); 240,-Nieskurzów-Podlesie, Góry Swiętokrzyskie, leg. J.S., 1980 (2^b); 242,-Kup near Opole, leg. J.S., 1980 (2^b); 245,-Kobyla Góra 243,-Nieskurzów-Podlesie, Góry Swiętokrzyskie, leg. J.S., 1980 (2^b);

near Ostrzeszów, leg. J.S., 1980 (2^b); 246,-Brzoza Królewska near Rzeszów, leg. J.S., 1980 (1^b, 2^b); 248,-Susiec, leg. J.S., 1981 (1^b); 296,-Ojców reserve, leg. R.Z., 1981 (1^b, 2^b); 297,-Góry Stołowe, leg. J.S., 1981 (1^b); 305,-Maszewo Lęborskie near Słupsk, leg. J.S., 1981 (2^b); 310,-Maszewo Lęborskie near Słupsk, leg. J.S., 1981 (2^b); 321,-Plitnica stream near Wałcz, leg. J.S., 1981 (1^b).

Note Added In Proof

After completing the manuscript, one of us (R.Z.) obtained artificial autopolyploids from all three forms of *Pellia epiphylla*, i.e. $PX1^a$, $PX2^a$, and PX3. It turned out that the length of the whole chromosome sets in these plants was exactly the same as in natural $n = 18$ plants, i.e. the relation of both lengths was also 1:1.6. Electrophoretic phenotypes were, however, exactly the same in $n = 9$ plants and in artificial polyploids: they did not show the difference described on page 205, caption 4.1.1.

Our new results show also that the northern *Pellia epiphylla* electromorph (PX3) differs from the rest of *Pellia epiphya–P. borealis* complex in nearly all enzymes studied.

See also:

Zielilnski, R. 1984a. Genetic variation and evolution of the liverwort genus *Pellia* with special reference to Central European territory. I. Electrophoretic evidence of cross-fertilization in the monoecious *Pellia epiphylla*, $n = 9$. Jour. Hattori Bot. Lab. 56: 255–262.

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Monogr. Syst. Bot. Missouri Bot. Gard. 11: 211—216. 1985.

BRYMELA TUTEZONA (MUSCI: HOOKERIACEAE), A NEW GENUS AND SPECIES FROM WESTERN PANAMA[1]

MARSHALL R. CROSBY[2] AND BRUCE H. ALLEN[2]

Abstract. A new moss genus and species, *Brymela tutezona* (Hookeriaceae), is described from western Panama. The genus appears closest to *Hookeriopsis* section *Omaliadelphus* (specifically *H. parkeriana*). It differs from that section by its greater size, non-complanate stems, ovate-lanceolate to ovate-acuminate leaves that are rounded to the insertion and shorter, broader alar cells.

The Republic of Panama is considered to contain the ". . . most diverse assemblage of plants and animals of any area of comparable size" (Raven, 1980). Within Panama the forested western highlands, combining sharp vertical relief with high rainfall, have proven to be an area of exceptional floristic interest. It is not surprising then that in working through the extensive Panamanian moss collections at the Missouri Botanical Garden we have come across a new moss, which we here name *Brymela tutezona*.

The type collection of *Brymela tutezona* was made in the province of Veraguas on the summit of Cerro Arizona (ca. 1500 m), in a remarkably moist habitat. The plants are epiphytic and were collected in the crowns of trees and shrubs of an elfin cloud forest. In testimony to the wetness of this region it has been reported that *Sphagnum* is a component of the epiphytic flora of the cloud forest.

Brymela tutezona Crosby & Allen gen. & sp. nov.

Genus et species novum, *Hookeriopsi* sectioni *Omaliadelpho* affini (*H. parkerianae* proximae), statura majore, absentia caulium complanatorum, foliis ovatis-lanceolatis vel ovatis-acuminatis et rotundatis insertioni, cellulisque alaribus brevibus, latis differt.

Plants robust (Fig. 1–2), creeping, glossy, epiphytic, yellow-green above, red to burgundy below. *Primary stems* red, adnate to substrate, epidermal cells 73–108 μm × 11.5–16.0 μm, rectangular, incrassate and porose, not storied; in cross section pachydermous throughout, 3–4 rows of small, incrassate, red-brown epidermal cells, a cortex of larger, thinner-walled, yellow cells, central strand absent. *Rhizoids* in sparse groups restricted to the substrate side of the stems, red-brown, smooth, end walls oblique. *Secondary stems* irregularly spaced, erect, to 11 cm long × 0.8–1.3 cm wide; secondary stems with numerous arrested primordia at regular intervals, but branches sparse and irregularly spaced. *Pseudoparaphyllia* absent. *Paraphyllia* absent. Stem and branch

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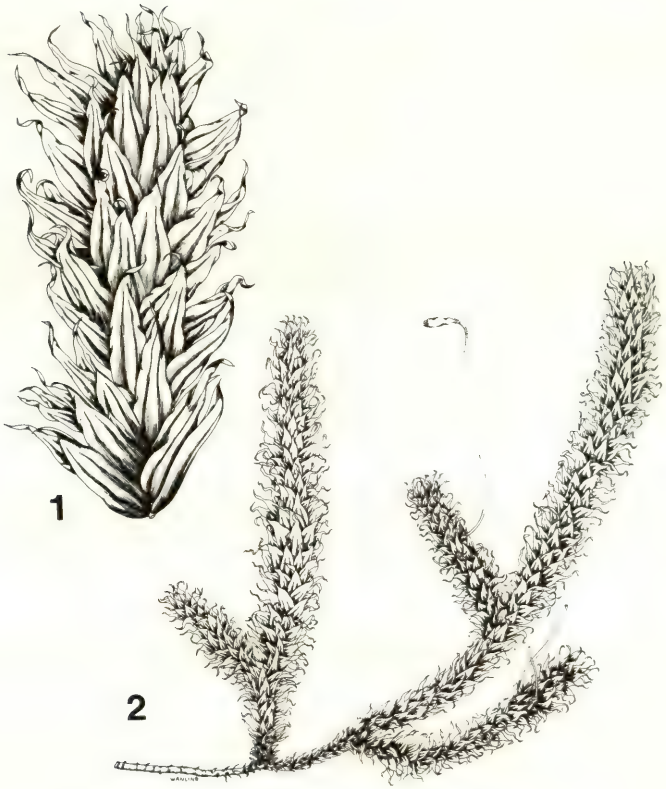
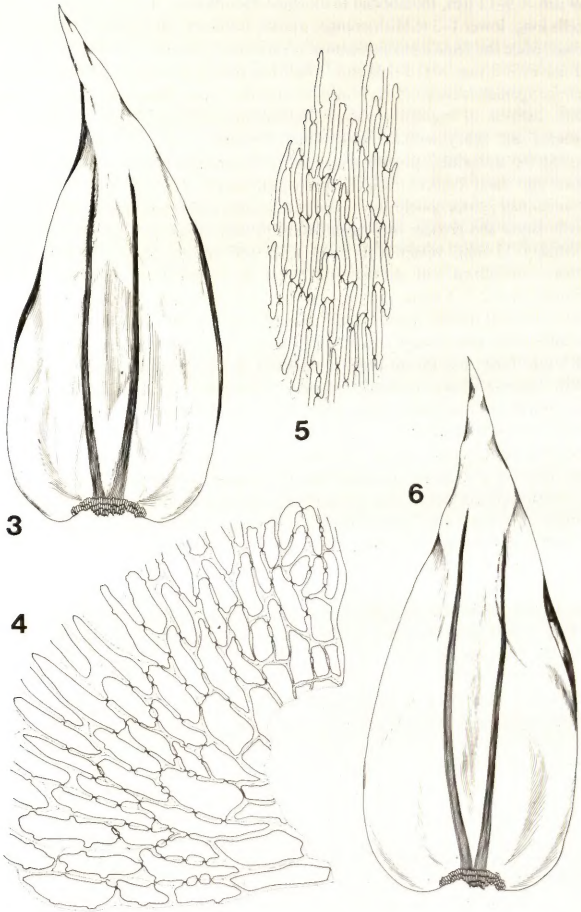


FIGURES 1–2. *Brymela tutezona*.—1. Habit, × 4.6—2. Habit, × 1.4.

leaves (Fig. 3, 6) similar, 6–8 mm × 2–3 mm, erect-spreading, broadly ovate-lanceolate to acuminate, weakly concave below, plane above, rounded to the insertation (at times weakly auriculate), more or less plicate at base, strongly undulate above, little changed wet or dry; margins plane, entire at base, weakly serrulate above. Costa double, united at base, strong through out, reaching ½–¾ the leaf length, with an A-type (see Kawai, 1968) cross-section. *Cells* smooth, incrassate, porose, reddish-orange in narrow band across the insertation; at the alar region (Fig. 4) 23–55 μm × 13–21 μm, shortly rectangular; median



FIGURES 3–6. *Brymela tutezona*.—3. Leaf, × 14.–4. Cells at alar region, × 252.—5. Cells at midleaf, × 240.—6. Leaf, × 14.

cells (Fig. 5) linear rhombodial, 55–115 μm × 7–9 μm; apical cells shorter and wider, 39–69 μm × 9–12 μm, rhombodial to elongate-rhombodial. *Axillary hairs* 7–8 per leaf, 2–4 cells long, lower 1–3 reddish-orange, square, terminal cell hyaline, narrowly elliptic. *Dioicous*. Male and female plants identical. *Perigonial buds* borne laterally, 2–4 mm long; lower leaves 2–3 mm × 0.5–1.0 mm, ovate-lanceolate, ecostate, cells as in vegetative leaves; perigonial leaves 0.5–1.3 mm × 0.2–0.5 mm, sheathing, ovate-acuminate, ecostate, cells as in vegetative leaves. *Antheridia* 0.62–0.87 mm × 0.07–0.12 mm, asymmetric and subcylindrical, stalk short, paraphyses 1.0–1.2 mm, at base of and surpassing the antheridia, all cells rectangular. *Perichaetia* terminal on lateral buds that elongate into short branches after fertilization; leaves 2.5–3.5 mm × 0.5–0.8 mm, ovate-acuminate, costa double, ½–¾ the leaf length, cells as in vegetative leaves except alar cells larger and broader in a more extensive area. *Archegonia* numerous, 0.75 mm long (stalk 0.12 mm, venter 0.10 mm, neck 0.53 mm), paraphyses 0.50–0.88 mm, numerous, intermixed with archegonia, lower 3–4 cells short, quadrate, upper cells rectangular. *Seta* 2.5–3.0 cm, dark red, smooth below, scabrous above; in cross-section 3–5 rows of small reddish-yellow, incrassate epidermal cells, a cortex of larger, yellow, firm-walled cells and a very small central strand of small thin-walled cells. *Capsule* 2.5–3.5 mm long, red to red-brown, scabrous at base, smooth above, more or less inclined, symmetric and cylindric, weakly constricted at base forming short neck; exothecial cells rounded-rectangular, incrassate, more or less collenchymatous. *Annulus* not observed. Superficial *stomata* present at base of capsule. *Operculum* not observed. *Peristome* diplolepideous, double. *Exostome* teeth 16, 0.70–0.75 mm long, 0.15 mm wide at base, inflexed when wet, reflexed when dry; dorsal surface red, furrowed, trabeculae thin, closely spaced, projecting beyond the lamellae giving the peristome a fringed appearance in surface view, lamellae with numerous, smooth, closely spaced, horizontal striae below, becoming thickly papillose at tips, median line present in furrow; ventral surface yellow, trabeculae thin, smooth, closely spaced, shortly projecting, lamellae smooth. *Endostome* yellow, lightly roughened; basal membrane 30 μm high, walls on ventral surface thickened and yellow, walls on dorsal surface thin, hyaline; processes 16, 30–40 μm high, not perforated; cilia absent. *Spores* spherical, 23–35 μm, lightly roughened. *Calyptra* not seen.

Type. PANAMA.Veraguas: N of Santa Fé, summit of Cerro Arizona, 1570 m, *Hammel 4740*. Holotype: MO. Isotypes: BM, DUKE, NICH, PMA.

Paratype. PANAMA. Veraguas: Mountains behind Escuela Alto de Piedra, beyond Santa Fé. On top of "Cerro Arizona" (=Cerro Tute of others?), 1533 m, *Hammel, Kress & Clarkson 8571*. Paratypes: ALTA, C, CANM, CHR, DUKE, FH, G, H, L, MICH, MO, NY, PMA, S.

Etymology. The generic name *Brymela* was composed by selecting and euphonically arranging letters from the name of the collector of the type, Barry Hammel, at that time a graduate student at DUKE and now a member of the staff at MO. The specific epithet *tutezona* is a combination of "tute" and "arizona," two names for the mountain on which the type collection was made.

Ecology. Epiphyte on leaves and branches in the crowns of trees and shrubs in elfin cloud forest.

Brymela is unhesitantly placed in the Hookeriaceae on the strength of its pleurocarpous habit, strong double costae, weakly differentiated alar region, lack of a central strand in the stem, absence of paraphyllia or pseudoparaphyllia, and double peristome having a hookeriaceous exostome but lacking endostomial cells. Other, more general, features *Brymela* shares with members of the Hookeriaceae include its dioicous sexual condition with similar male and female plants, scabrose seta, and collenchymatous exothecial cells.

The genus represents one of the largest mosses found in the Hookeriaceae (*sensu* Crosby, 1974). Although its robust size (branches to 11 cm) is approached by other species in the family (e.g. *Thamniopsis pendula* has stems to 12 cm, Welch, 1976) most of those are strongly complanate. In *Brymela* the stems and branches have leaves thickly borne on all sides giving the plants a macroscopic appearance similar to some species of *Ptychomnion*.

Plants of *Brymela tutezona* have strongly creeping primary stems and erect, robust secondary stems that only occasionally bear branches. On stripping the leaves from most plants, however, numerous primordia have been found at regular intervals along the secondary stems. Since fertile plants have been observed with numerous perigonia or perichaetia at regular intervals along the secondary stems, it would seem that the regularly spaced primordia may represent incipient perichaetial or perigonial buds rather than branch buds.

Brymela tutezona presents a number of unusual features. The leaves are rounded to the insertion, at times appearing weakly auriculate. The cells throughout the plant (stems, leaves, setae, and capsules) are remarkably incrassate and porose. The presence of incrassate and porose epidermal cells, arranged in a non-storied manner, and thick-walled cortical cells give the stems a stiffness not common in the Hookeriaceae. The cells in the reproductive leaves are also thick-walled and porose throughout, and, while strong double costae are present in the perichaetial leaves, the perigonial leaves are ecostate. The antheridia are remarkably long (0.6–0.8 mm), although this may simply be a reflection on the overall large size of the plants.

The robust, non-complanate habit of *Brymela*, its strong double costae, smooth, elongate leaf cells and unbordered leaves that are not dimorphic represents a combination of characteristics found in few Hookeriaceae genera. *Brymela* resembles *Hemiragis* in its robust, non-complanate habit, incrassate and porose leaf cells, and the tendency of its leaves to be plicate at the base as well as rounded to the insertation. However, its strongly undulate, ovate-lanceolate leaves in conjunction with its thick-walled leaf cells and strong costa indicates a closer relationship with *Hookeriopsis*.

Based on its robust size, dioicous sexual condition, strongly undulate leaves, entire costa, smooth, incrassate leaf cells, weakly serrulate leaf margins, and scabrous seta *Brymela* is nearest *Hookeriopsis* section *Omaliadelphus*. Within section *Omaliadelphus*, *Brymela tutezona* is comparable to *Hookeriopsis parkeriana*, a robust moss with weakly complanate stems, strongly undulate, lanceolate-acute leaves, incrassate and porose leaf cells, weakly serrulate leaves and an entire costa. *Brymela tutezona* differs from *Hook-*

eriopsis parkeriana by its even greater size, complete lack of complanate stems, ovate-lanceolate to ovate-acuminate leaves and its leaves that are rounded to the insertion (at times weakly auriculate) with shorter and broader (but still incrassate and porose) alar cells.

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